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Postconflict and conflict behavior in all-male groups of captive western lowland gorillas (Gorilla gorilla gorilla)

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ABSTRACT

I studied male western lowland gorillas (*Gorilla gorilla gorilla*) in a captive setting in order to determine if post-conflict reconciliation exists in male-male dyads of this species. I also examined conflict itself in order to determine the consequences of housing these males together in all-male groups in captivity. This was accomplished by examining the behaviors of nine male gorillas at the Henry-Doorly Zoo in Omaha, Nebraska. Data that I recorded included post-conflict observations, social interactions, and activity budgets. I analyzed the data in order to determine levels of reconciliation, welfare of the population, and comparisons with wild conspecifics. I hypothesized that males in this species would differ from mountain gorillas (*Gorilla gorilla beringei*) based on ecological and species' variations: that they would exhibit reconciliation. I rejected this hypothesis. However, lack of observed conflict between those individuals comprising 'valuable' relationships suggests that further study be done in order to examine whether postconflict reconciliation exists in this type of social setting. Results on conflict itself show that the age of the youngest in a dyad determines the characteristics of that relationship. In particular, affiliation levels all but diminish once the age of the youngest in a dyad reaches twelve years, which is also the approximate silverback transition period for male gorillas. In addition, conflict begins to appear, where it was almost non-existent before, at this critical age. Because male gorillas in the wild generally separate themselves from other adult males around this age (to become solitary or form their own one-male group), it is not surprising, then, that conflict should ensue in captivity where natural emigrations cannot occur. Therefore, I suggest that captive all-male gorilla groups may not form a long-term solution to the 'surplus' of male gorillas in captivity.

CHAPTER 1. INTRODUCTION

1.1 Overview

Group living is a widespread phenomenon that occurs across various animal species (Parrish & Edelstein-Keshet 1999; Aureli et al. 2002) and typifies primates in general. However, sociality brings with it a number of related costs and benefits (Terborgh 1986; Garber 1987; Noe & Bshary 1997; Gillespie 2001; Steenbeek & van Schaik 2001). Among the costs of group living are expected conflicts of interest that may ultimately result in detrimental effects for both the individuals involved and their group (Aureli et al. 2002, Arnold & Aureli 2007). For example, the most common types of conflicts include competition for limited resources - such as mates or food - and disagreements about decisions, such as how much time should be devoted to different activities, or in which direction to travel (Aureli & de Waal 2000). Therefore, to balance the disruptive consequences of social grouping, and to maintain beneficial relationships, it is necessary for species to engage in reconciliations (de Waal 2000b) that will both put an end to conflict and restore peaceful interactions (Silk 1997; Aureli et al. 2002).

The need for conflict resolution is apparent in humans and non-humans alike (Aureli & de Waal 2000). In fact, developments in post-conflict resolution and relationship maintenance in non-human primates may have significant implications for applied animal management as well. However, to date, most studies involving these behaviors have focused on select primate species (Bjornsdotter et al. 2000; Aureli et al. 2002), leaving other species understudied (Verbeek & de Waal 1997; Arnold & Barton 2001). One such species is the western lowland gorilla (*Gorilla gorilla gorilla*), where currently only one study by

Mallavarapu and colleagues (2006) has been published. However, this research was limited in that it did not include male-male interactions. Although previous work on mountain gorillas (*Gorilla beringei beringei*, Watts 1995a,b) suggests that postconflict reconciliation is absent in male-male dyads, no research to date has been conducted on such behavior in all-male groups of captive western lowland gorillas (Mallavarapu et al. 2006).

The majority of information on gorillas stems from research conducted on mountain gorillas, consequently leaving much about western lowland gorillas unknown (Parnell 2002; Bradley et al. 2004; Robbins et al. 2004; Robbins 2007). However, because western lowland gorillas are the most common gorilla species in captivity, it is vital that their social dynamics be understood for better captive management (Stoinski et al. 2001). In addition, because of an increase in single-male, multi-female groups in captivity (as opposed to male-female pairs), zoos are beginning to face the problem of 'surplus' males (Stoinski et al. 2001). This problem is currently being dealt with by establishing a growing number of all-male or "nonbreeding groups" (Gatti et al. 2004) in captivity (Stoinski et al. 2004). However, because escalated aggression is a growing problem among blackback and silverback males in all-male groups (personal communication with zoo veterinarian D. Armstrong; personal observations), it is important that those involved in captive management strategies better understand these conflicts in order to provide for the most optimal group housing situations.

My study will be the first to investigate postconflict behaviors of western lowland gorillas living in all-male groups in captivity. These investigations may not only lend further insight into the understanding of primate social systems but have implications for captive management strategies as well.

1.2 Conflict in Gorilla Society

Before information on postconflict behavior is presented, it is first beneficial to briefly examine conflict in gorilla society. Access to resources, primarily food, is what differentiates female success in a group; whereas access to mates is what differentiates males (Harcourt & Stewart 2007). In essence, females compete by surviving and rearing offspring, while males compete through mating.

Female gorillas compete over food. In fact, Harcourt and Stewart (2007) found that more than 75% of all conflicts among females were over food. These incidents ranged from supplants and mild threats to actual attacks. Watts (1994) found similar results, where about half of all aggression among females in his four study groups was over food. In 44% of conflicts, in two of the groups, at least one of the protagonists was wounded, indicating that aggression among females can be fierce (Watts 1994).

After food, the next most common context for aggression among female gorillas is labeled as unprovoked harassment, where no resource seems to be involved. Harcourt and Stewart (2007) observed that one female simply threatens another, possibly asserting her dominance toward subordinates. Consequently, threatened subordinates remain subordinate. They suggest that the benefit of these reminders is to allow easier access to a resource for the dominant opponent the *next* time these individuals compete. Therefore, food may still be playing a major role in these alternative contexts.

The distribution of food has also been shown to affect competition among gorillas. In a captive study Scott & Lockard (2006) found that female gorillas increase aggressive competition when food is clumped. Subsequently, dominant individuals elevated aggression toward subordinates, and subordinates increased submission. This captive study may be

more indicative of a western lowland gorilla environment (as opposed to mountain gorilla ecology) due to higher levels of frugivory and what is assumed to be clumped resources in the former.

Gorilla females in larger groups also face increased feeding competition. Watts (1985) found that females encountered more feeding interruptions per hour of observation in larger groups. In fact, the same female in a larger group was involved in more competition than when she was in a smaller group. If larger groups mean more competition, then females should be particularly aggressive to newcomers, and they are. Gorilla female residents and immigrants are almost one-and-a-half times as frequently aggressive to each other as are unrelated residents within a group (Watts1994). Results from a captive study (Hoff et al. 1996) show similar results, with changes in group membership being met with escalated levels of aggression.

In regard to female gorillas, it seems that at least in large groups competition occurs often enough for contrasts in ability to be present (Harcourt & Stewart 2007). However, those differences are unimportant for many females (Watts 2001). In other words, winning or losing in contest competition (among females) does not significantly alter these individual's ability to survive, mate or reproduce. This is largely due to the fact that any competition a female faces from another female will be minimal by comparison to the competition she faces from a male (Harcourt & Stewart 2007).

An important component to gorilla society is the absolute dominance of the male over females. As Harcourt and Stewart (2007) state, this is largely the result of the male being twice their size. As their studies have shown, the male in a gorilla group supplants the average female nearly ten times more often than the average of the other females within the

group (Harcourt & Stewart 2007). In fact, the effect of the male is so strong that group size is unlikely to be limited by competition among females, because by comparison, an extra female makes so little difference to the competition already imposed by the one male within the group. Therefore, not only are males the most frequent competitors that females face, they are, ultimately, an unbeatable competitor compared to other females.

Competition among male gorillas, in contrast to females, is determined by a different kind of resource. Here, mates are the major resource for males, and it is these females that distinguish the unsuccessful from the successful male. As Harcourt and Stewart (2007) point out, the relatively thin distribution of female gorillas in an environment affects the distribution of males. It requires that these males stay with females, instead of roaming in search of them. Alternatively, one form of mating competition among males, infanticide, forces females to associate with a protective male, instead of roaming alone.

Most conflict among male gorillas within a multi-male group is mild. As Robbins (1996) observed, males display at one another, or just cough grunt or lunge without actually touching. Intergroup aggression among gorilla males can be somewhat different. Encounters between groups, or between groups and solitary males (both considered a unit), are potentially important circumstances in gorilla society because these are times when females transfer and when males compete most intensely (Harcourt & Stewart 2007). Specifically, interunit encounters last from around thirty minutes to one or two days (Sicotte 2001), but can extend for much longer, up to a week or more (Watts 1994). They usually end with the participants going their separate ways, but sometimes one group might supplant or chase the other group away (Watts 1994; Levrero 2001). Intense agonistic encounters can also

influence ranging patterns of groups or lone males as they flee from or pursue one other (Watts 1998).

Encounters between gorilla social units vary in their nature from peaceful to lethally aggressive. However, most encounters observed involved at least some form of agonistic response: either avoidance/flight, or contact/non-contact aggression (Doran-Sheehy et al. 2004; Harcourt 1978). During these interunit conflicts, opposing silverbacks usually exchange aggressive displays including hooting, chest-beating, stiff-legged strutting during which lips are pursed, and spectacular runs, ground thumps, and foliage whacks (Harcourt 1978; Sicotte 1993). Although silverbacks are the primary protagonists in these conflicts, other group members, such as subadult males and blackbacks, sometimes join in with struts, runs or chest-beats (Harcourt & Stewart 2007).

While most interunit encounters involve only threat displays, some escalate into physical aggression between gorilla males, which occasionally leads to serious injury or death (Fossey 1983; Harcourt 1978; Watts 1994). For example, in the Virungas, 24% of encounters within 50 meters involved males hitting or biting one another (Sicotte 1993). On the other hand, some group members, including adult males, occasionally ignore one another and sometimes intermingle as one group (Doran-Sheehy et al. 2004; Harcourt 1978; Sicotte 2001). These peaceful encounters appear to be more common among western lowland gorillas where groups may be more tolerant of each other due to relatedness or repeated exposure in swampy clearings (Doran & McNeilage 2001).

1.3 Postconflict Behavior

To better understand the mechanisms that underlie conflict resolution in gorillas, it is first beneficial to analyze postconflict behavior in primates in general. The most common causes of conflict in primate species can be attributed to competition over limited resources (Terborgh & Janson 1986; Steenbeek & van Schaik 2001). For primates that live in groups, however, these conflicts may compromise the benefits of group living, especially if they escalate into aggression (Aureli et al. 2002). Therefore, according to Silk (2002), reconciliation may be favored by natural selection because it has the ability to settle conflicts promptly and in an unambiguous manner, and this is useful because agonistic interactions can have abrupt beginnings but possibly indefinite endings. In addition, postconflict interactions can serve as signals that the aggressive action will stop, and that peaceful interactions will ensue (Silk 1997). Other benefits of postconflict reconciliation suggest that primates can reduce elevated levels of anxiety and uncertainty instigated by conflict (Castles et al. 1999; Silk 2002; Cooper et al. 2006), as well as restore valuable relationships (Cheney et al. 1995; Castles et al. 1996; Arnold & Barton 2000; Aureli et al. 2002).

Two important hypotheses regarding why postconflict reconciliation is such a widespread phenomenon are described by Aureli and colleagues (1989; 1991) as the *uncertainty reduction hypothesis* and by de Waal and Aureli (1997) as the *valuable relationships hypothesis*. The former states that self-directed, or stressful, behaviors are reduced after reconciliation is achieved. This reduction is explained by a decrease in uncertainty in the former opponents regarding the status of the relationship. The *valuable relationships hypothesis* stresses the importance of relationship quality in determining which dyads will be most likely to reconcile. For instance, the relationships that provide the most

fitness benefits for both parties are those opponents that are more likely to reconcile. Therefore, what an individual can offer (value), the measure of friendly interactions between the opponents compared to aggressiveness (compatibility), and the probability that the relationship will not change for the worse (security) are three vital components of this hypothesis.

Most studies of reconciliation among primates have shown that positive interactions between former opponents will occur sooner after a conflict than compared to control periods (Silk et al. 1996; Call et al. 1999; Preuschoft et al. 2000; Aureli et al. 2002; Arnold & Aureli 2007). However, in light of this seemingly widespread phenomenon among non-human primates, there also exists an astounding amount of diversity in conflict management patterns (Aureli & de Waal 2000; Arnold & Aureli 2007) that results in a variety of postconflict friendly behaviors (Aureli et al. 2002). In some species, conspicuous behavior patterns, which are rarely used outside the postconflict context, constitute reconciliation (Aureli et al. 2002; Arnold & Aureli 2007). These are termed *explicit reconciliations* and can be seen among a variety of macaque species, such as pig-tail macaques (*Macaca nemestrina*) (Castles et al. 1996), as well as leaf monkeys (*Trachypitecus obscurus*) (Arnold & Barton 2001), where individuals may embrace one another or perform hold-bottom rituals. *Implicit reconciliations*, on the other hand, are affiliative behaviors that are regularly observed in other contexts. These include behaviors like allogrooming or making body contact, which is seen in chimpanzees (*Pan troglodytes*) (Preuschoft et al. 2002). Variation in reconciliation is observed between groups of the same species as well (Castles et al. 1996; Aureli et al. 2002; Arnold & Aureli 2007). For example, Castes and colleagues (1996) found that two groups of

pig-tail macaques appeared to differ in their 'method' of reconciliation; where one group displayed a 'standing grasp' postconflict behavior and the other group did not.

Developmental and environmental influences can also contribute to the variations found among individuals and species of primates, suggesting that the social environment has an important role to play in influencing reconciliation behavior (Arnold & Aureli 2007). For example, the absence of social experience can result in an inability to reconcile. Ljungberg and Westlund (2000) found that rhesus macaques (*M. mulatta*) who had been separated from their mothers before weaning, then hand-reared, and housed singly for extended periods did not show any form of reconciliation; this was in contrast to individuals who were housed in peer groups at an early age. Another study, which examined the effects of cohousing on reconciliation among more tolerant/conciliatory stump-tailed (*M. arctoides*) and less conciliatory rhesus macaques, also found environmental influences (de Waal & Jahanowicz 1993). This experiment found that after a period of six weeks of housing two species together, the conciliatory tendencies of the rhesus macaques gradually rose to the level of the stump-tailed macaques, once again showing that the environment can contribute to variations in reconciliatory tendencies.

Certain forms of reconciliation found within some species of primates are more subtle (Aureli et al. 2002; Arnold & Aureli 2007). For example, in chacma baboons (*Papio hamadryas ursinus*) soft vocalizations, such as grunts, serve to facilitate friendly interactions following conflict (Cheney et al. 1995; Silk et al. 1996). Even more subtle behaviors, such as spatial positioning or proximity, can serve to restore relationships after conflict in black-and-white guereza (*Colobus guereza*) (Bjornsdotter et al. 2000), stump-tailed macaques (Call et al. 1999), and western lowland gorillas (Mallavarapu et al. 2006). This suggests that

interactions involving close proximity, rather than actual physical contact, may be the main mechanism for resolving conflicts in some primate species (Mallavarapu et al. 2006).

Reconciliation not only varies between species and groups of primates but between the sexes as well (Watts 1995a; Sommer et al. 2002; Cooper et al. 2006). For example, Bonnet macaques (*M. radiata*) showed significantly higher reconciliation rates between female-female dyads, as opposed to female-male or male-male dyads (Cooper et al. 2006). Similar results were found in Indian langur monkeys (*Semnopithecus* [*Presbytis*] *entellus entellus*) where female-female dyads showed much greater postconflict affinity than both male-female or male-male dyads (where the latter two relationships were absent in reconciliation) (Sommer et al. 2002). These findings are most likely correlates of primate groups where close kinships exist among females (Sommer et al. 2002) and where females frequently groom, embrace and huddle together in non-conflict contexts (Cooper et al. 2006).

Variation in sex differences in reconciliation also occurs among mountain gorillas, where only male-female dyads have been observed to engage in postconflict behaviors (Watts 1995a). Because bonds between females and between males are observed to be rather weak, it is not surprising that reconciliation between these dyads could not be demonstrated. In fact, females often continue to interact aggressively after initial conflicts until they move away from one another (Watts 1995a). In contrast, because female-male relationships are the basis of mountain gorilla societies, reconciliation between the two is common (Watts 2001). It cannot be assumed, however, that these results will be typical all species of gorilla. In fact, the foraging strategy, resource availability, and habitat type of mountain gorillas contrast significantly with that of western lowland gorillas, leading some to believe that a variation in social behavior may exist as well (Doran & McNeilage 2001). The fact that western lowland

gorillas depend on more clumped fruit resources in their diet, as opposed to the more evenly distributed herbaceous diets of mountain gorillas, suggests that the latter may not provide a universal model for all gorilla species when examining social behavior (Sterck et al. 1997; Doran & McNeilage 2001).

Therefore, in this study, I examine post-conflict behavior in male-male interactions of captive western lowland gorillas in order to determine if species variation will produce similar variation in behavior among male gorillas. To accomplish this, I studied 9 male western lowland gorillas in all-male groups in captivity, in order to examine conflict and post-conflict behaviors in the species. I hypothesized, then, that the variations found between mountain and western lowland gorillas suggest differing results when it comes to reconciliation. In other words, I predicted that some version of reconciliation exists among western lowland male gorillas.

CHAPTER 2. LITERATURE REVIEW

Wild gorillas are currently found in ten central African countries. They live in a diversity of habitats that range from Afromontane rainforests to coastal lowland forests. There are four major taxonomic classifications of gorillas, which correspond to their geographic location and habitat type. They include the western gorillas *Gorilla gorilla gorilla* and *Gorilla gorilla diehli* (western lowland and Cross River gorillas, respectively), as well as the eastern gorillas *Gorilla beringei graueri* and *Gorilla beringei beringei* (eastern lowland and mountain gorilla). Age classifications typically used for gorillas include infants (0-3.5 years), juveniles (3.5-6 years), subadults (6-8 years), adult females (>8 years), blackback males (8-12 years), and silverback males (>12 years) (Robbins 2007). As blackbacks develop into silverbacks a number of secondary sexual characteristics emerge. For instance, the hair on their backs becomes shorter and gradually turns silvery white, an enormous sagittal crest emerges along with nuchal crests (on their skull) for attachment of jaw muscles, and relatively large canines emerge (Harcourt & Stewart 2007). Though gorillas usually reside in stable, cohesive social units, group structure may vary. For example, these individuals may reside in one-male, multi-male, or all-male groups, or may even be solitary for a time.

2.1 The Sociality of Gorillas

Introduction

Through the interactions of phylogeny, ecological variables, social factors, and demographic and life history variables, primates have evolved to develop significant

variations in their social systems (Smuts et al. 1987). Because western lowland and mountain gorillas differ significantly in their foraging strategy, resource availability, and habitat type, their genus (*Gorilla*) can provide researchers with a unique opportunity to examine current proposed models of social organization (Sterck et al. 1997; Doran & McNeilage 2001). For example, the western lowland gorilla occupies western central Africa in the countries of Equatorial Guinea, Gabon, Angola, Cameroon, Central African Republic, and the Republic of Congo (Robbins 2007). This species is, in contrast, broadly geographically separated from mountain gorillas, which are found in the eastern central African countries of Rwanda, Uganda, and the Democratic Republic of Congo (Robbins 2007). Although western lowland gorillas comprise the majority of the existing gorilla population today, the greater part of studies to date have concentrated on the pioneering work of Dian Fossey and subsequent researchers at the Karisoke site in Rwanda, on mountain gorillas (Doran-Sheehy & Boesch 2004; Yamagiwa & Kahekwa 2001; Robbins et al. 2004). This comparatively small population of gorillas occur in a habitat that is quite distinct from gorillas elsewhere (Doran & Mc Neilage 2001; Robbins et al. 2004). Until recently, though, it has generally been assumed that the behaviors of mountain gorillas are typical of all gorillas. However, with increasing research on western and eastern lowland gorillas (Tutin 1996; Parnell 2002; Gatti et al. 2004; Yamagiwa et al. 2003), scientists are finding striking indicators of variability in gorilla behavior (Doran & McNeilage 1997; Tutin & Vedder 2001; Robbins 2007).

The goal of the next section is to examine the variability in gorilla behavior between mountain and western lowland species by examining the ecological and social factors

influencing gorillas in each unique habitat. Through this analysis one might better understand the factors that influence diversity in primate social systems, beyond the mere classification of 'gorilla'. The following section, then, will briefly outline general social relationships found in gorilla groups. Here, the emphasis will be on mountain gorillas due to the greater amount of data currently available on this species.

Variation in Ecology and Social Behavior: Mountain vs. Western Lowland Gorillas

Mountain Gorilla Behavior

The most extensively studied mountain gorillas live in the high-altitude montane forests of Rwanda (Doran & McNeilage 2001). They are herbivorous, feeding mostly on shoots, stems, leaves, and piths of terrestrial herbs (Fossey & Harcourt 1977; Vedder 1984; Watts 1996), whose availability varies little seasonally (Watts 1996). Mountain gorillas are selective in their feeding behavior, choosing vegetation that is relatively high in protein and low in tannins. These higher-quality terrestrial herbs are both abundant and widely distributed, which leads to minimal within-group feeding competition (Vedder 1984; Watts 1984; Rogers et al. 2004).

Mountain gorillas are primarily found in stable, cohesive social units, although adult males can be solitary (Robbins 2007). The majority of these groups include one adult male, although up to four males may be present (Harcourt 1979; Robbins 1995; Watts 1996). This type of group structure, with more than one silverback present, is often the result of males maturing and remaining within their 'father's' group (Robbins 1995). A third type, all-male groups, can form through the merger of immature males that may have been evicted from a "breeding" group by a dominant silverback (Robbins 1995; Gatti et al. 2004).

The average group size of mountain gorillas ranges from two to over 40 individuals, with 8-10 being the average (Parnell 2002; Gatti et al. 2004). In fact, the number of groups with over 20 individuals has been increasing in the last 30 years, which may be the result of increased protection and decreased poaching (Kalpers et al. 2003). Within groups, adult social bonds are strongest between females and silverbacks, whereas most females are unrelated and do not associate on a regular basis with one another (Watts 2001). Based on low levels of affiliation, silverback relationships (with one another) also appear weak (Robbins 2007).

Rare among Old World anthropoids, both male and female gorillas may be philopatric, or disperse (Harcourt et al. 1976; Tutin 1996). Females disperse during inter-group encounters and relocate directly into other groups. Maturing males, on the other hand, might become solitary or join all-male groups (Harcourt 1978). In mountain gorillas, where feeding competition is low, females show no group size preferences for dispersal but do prefer multimale groups as opposed to one-male groups and solitary males (Watts 2000). Subordinate silverbacks emigrate at approximately 12–18 years of age, often to become solitary males (Robbins 1995; Stokes et al. 2003; Yamagiwa & Kahekwa 2001). However, multimale groups are more common in mountain gorillas, where male emigration is lower, than in western lowland gorillas (Parnell 2002; Gatti et al. 2004; Robbins 2004).

It is presumed that female gorillas form long-term relationships with males in order to avoid infanticide by extragroup males (Watts 2000; van Schaik & Kalpers et al. 2003) and to benefit from protection against predators (Robbins 2007). Despite this, infanticide accounts for at least 37% of infant mortality in mountain gorillas (Watts 1989) and is more common in one-male groups compared to multimale groups (Robbins 1995). This is because most

infanticide occurs after the death of a silverback in a one-male group when a new male (from outside the group) takes over and kills the unweaned offspring (Watts 1989).

Western lowland gorilla behavior

Western lowland gorillas are found in lowland tropical forests where the distribution and abundance of available food is considerably different from that of mountain gorilla habitats (Doran & McNeilage 2001; Robbins et al. 2004). Three chief differences in food availability exist between these two species' habitats. The first is that preferred high-quality terrestrial herbs are less abundant and more sparsely distributed in lowland forests (Watts 1984; Fay 1997). Second, either superabundant patches of Marantaceae forest or aquatic herbs are found in some, but not all western gorilla habitats (Doran & McNeilage 2001). The third difference lies in the increased amount of fruit available to western lowland gorillas (Goldsmith 2003; Ganas et al. 2004).

On a larger scale, there remains considerably more seasonality in the diets of western lowland gorillas compared to mountain gorillas (Rogers et al. 1988; Goldsmith 1996; Tutin 1996). When resources are abundant, fruit seems to comprise the majority of the diet in the former. However, when resources are scarce, and succulent fruit (ripe, sweet fruit that is low in protein and fat) is unavailable, there is an increase in consumption of low quality herbs, bark, woody pith and non-preferred fruits (Doran & McNeilage 2001). These fruits contain more fiber and tannins than preferred fruits and are usually ignored when ripe, succulent fruits are available (Rogers et al. 1988; Tutin et al. 1991). The number of differences in ecological variables found between western lowland and mountain gorilla habitats is predicted to result in a number of behavioral differences between these two species (Doran & McNeilage 2001; Doran-Sheehy & Boesch 2004; Robbins et al. 2004).

The overall social structure of western lowland and mountain gorillas appears to be roughly similar (Doran & McNeilage 2001), with groups in each species relatively equal in size (Gatti et al. 2004; Parnell 2004), although average group size does vary across sites (Kalpers et al. 2003; Parnell 2004). This is evident despite the reduced herb density and increased frugivory at western lowland gorillas sites (Doran & Mc Neilage 2001). However, data on group composition suggests that multimale groups of western lowland gorillas occur much less frequently than in mountain gorillas. Consequently, the majority of western lowland gorillas appear to reside in mostly one-male groups, or as solitary males (Parnell 2002; Gatti et al. 2004). Recent data by Gatti and colleagues (2004) has also shown that, like mountain gorillas, western lowland gorillas can also be found in non-breeding, all-male groups. They found that these groups can last for several years, although they are subject to frequent membership changes due to male migrations (which are much more common in western lowland gorillas). They suggest that immature males leaving their group can benefit from joining other males, as opposed to becoming solitary. Robbins (2001) states that in doing so gorillas will probably gain protection against predators and learn to develop better social relationships while maturing toward adulthood.

Average day ranges of western lowland gorillas suggest they average from two to five times longer than those of mountain gorillas (Tutin 1996; Goldsmith 1999). This is thought to be attributed to the need for fruit acquisition by gorillas in the lowlands (Cipolletta 2004; Doran-Sheehy et al. 2004). A more frugivorous diet, in fact, should affect the travel distances of primates because fruit resources are typically more dispersed in the environment, compared to herbaceous vegetation (Janson & Goldsmith 1995). In accordance with this hypothesis, various studies have shown a positive relationship between the degree of

frugivory and daily travel distance of gorillas (Doran-Sheeny et al. 2004; Ganas & Robbins 2005; Goldsmith 1999), with Karisoke mountain gorillas traveling only approximately 0.5 km/day and western gorillas traveling 1-2 km/day (Watts 1991; Cipolletta 2004).

Mountain gorilla home range size varies from 3 to 22 square kilometers (Watts 1984; McNeilage 2001; Ganas et al. 2004). This is in contrast to the larger home ranges (11-22 square km) of western lowland gorillas (Tutin 1996; Cipolletta 2004; Doran-Sheehy et al. 2004). Though both groups have extensive overlap in their home ranges, western lowland gorillas more commonly use the same home range at the same time (Doran & McNeilage 2001). This more frequent home range overlap and concurrent use of limited resources results in a much greater potential for inter-group encounters in western lowland gorillas compared to mountain gorillas (Bradley et al. 2004). In fact, Doran-Sheehy and colleagues (2004) found interactions between groups or lone males to occur a minimum of four times more frequently in western lowland gorillas, compared to mountain gorillas at Karisoke (Sicotte 2001).

The increased frequency of interactions among western lowland gorillas has not, as might have been expected, led to an increase in aggression between groups (Olejniczak 1996; Bradley et al. 2004; Doran-Sheeny et al. 2004). Although there have been reports of peaceful interactions between mountain gorilla groups (Sicotte 1993), these interactions are rare and account for only 7% of encounters. In contrast, studies of western lowland gorillas indicate that their encounters were more calm (Olejniczak; Parnell 2002; Bradley et al. 2004; Doran Sheeny et al. 2004), including peaceful intermingling and even co-nesting between groups (Bermejo 1997). Doran and McNeilage (2001) suggest that since these peaceful encounters have been noted at so many sites, it may be a more common phenomenon in western lowland

gorillas compared to mountain gorillas. Bradley and colleagues (2004) hypothesized that this may be due to males interacting differently with relatives and nonrelatives occupying neighboring home ranges.

A final comparative look at gorillas examines previously proposed reasons for group cohesion based on infanticide avoidance (Watts 1990; van Schaik 1996). However, as Doran and McNeilage (2001) point out, western lowland gorilla sociality (relative to that of mountain gorillas) appears to simultaneously produce an increased opportunity and decreased risk for those males who would attempt to commit infanticide. They suggest, first, that increased inter-group encounter rates with males should result in increased opportunities for these males to engage in direct male-male competition, including the opportunity for males to commit infanticide. Second, longer inter-birth intervals for western lowland gorillas compared to mountain gorillas (possibly the result of an increased seasonal variability in resources such as fruit, with reduced herb density) would seem to result in longer periods of infancy and thus higher vulnerability to infanticide (Janson & van Schaik 1993; van Schaik et al. 1999). Third, since the group male (and presumed sire) may be at a considerable distance from any given female as a result of reduced group cohesion (or increased group spread) among western lowland gorillas, males will be less able to defend females' infants from infanticidal males (Doran & McNeilage 2001).

Despite a greater potential for infanticide among western lowland gorillas, researchers have found that this species occurs more frequently in one-male groups (Parnell 2002; Gatti et al. 2004). This is despite the fact that long-term demographic studies of mountain gorillas have shown that infants born into these types of groups face a greater risk of infanticide than those of multimale groups (Watts 1989; Robbins 1995). In addition, with

more friendly encounters between western lowland gorilla groups, and no actual observed infanticides in this species (but see Stokes et al. 2003 for two inferred instances), the question of exactly why western lowland gorilla females would even remain in groups, *if* their primary reason is for infanticidal avoidance is raised (Harcourt & Greenberg 2001; Doran & McNeilage 2001).

Summary

A brief review of the subspecific variation in gorilla behavior has been made in order to reflect on whether changes in resource availability influence western gorilla behavior relative to that of mountain gorillas. Decreased herb density and increased fruit availability (as in western lowland gorilla sites) are seen, as predicted, to increase day ranges. In addition, although mountain and western gorilla groups may be similar in size, there is evidence that western lowland gorillas may be more flexible in their grouping patterns in response to changing resource availability. Increased frugivory appears to result in more contemporaneous overlap of home ranges between western lowland gorillas and more frequent encounters with other groups. These, among other factors, raise the question of whether infanticide avoidance by females acts as strongly as a selective factor in gorilla behavior as has been previously suggested (Doran & McNeilage 2001).

Social Relationships

Male social relationships

Research at Karisoke Research Center, Rwanda, has benefited significantly from the long-term monitoring of several neighboring mountain gorilla groups for over 30 years (Robbins 2001). This, combined with the little existing data on western lowland gorilla

social relationships, shifts our focus in this section back to mountain gorillas as the primary example for gorilla social systems in the wild (Robbins 2007).

Male primates often form weak relationships with one another, and gorillas are no exception (van Hooff & van Schaik, 1992, 1994; Kappeler 2000). This is thought to exist because males are competing for access to females, a resource that is not readily shared. Male philopatry may encourage affiliative relationships among male kin; however kinship is neither a guarantee nor a prerequisite for strong male-male bonds to form (van Hooff & van Schaik 1994; Kappeler 2000).

Mountain gorillas are said to have an age-graded social structure, even though rank does not always positively correlate with age (Harcourt 1979; Sicotte 1994; Watts 1992; Robbins 1996). Individuals reside in, or transition between, one-male, multimale, and all-male groups, in addition to residing as solitary individuals (Eisenberg et al. 1972; Yamagiwa 1987; Robbins 1995). According to this model, one-male groups form when a solitary silverback (adult male) acquires females from other groups. When other males in the group reach maturity, at approximately 13 years of age (Robbins 2001), the group is then labeled a multimale group. If a silverback in a multimale group dies, the group either remains as a multimale group or returns to a one-male group. If the males that remain cannot maintain the group, then females will disband and join other groups. Maturing males from heterosexual groups may also join all-male groups, and males may emigrate from either of these groups to become solitary (Robbins 2001).

Early studies of male mountain gorillas focused primarily on the relationship between silverbacks (adult males, over 12 years of age) and blackbacks (maturing males, age 8-12 years) because of the study groups' composition at the time (Harcourt 1979; Harcourt &

Stewart 1981). From these studies we learned that silverbacks are always dominant over blackbacks (Robbins 2007). In fact, blackbacks often spend their time at the periphery of the group, perhaps to avoid competition with adult females and silverbacks (Robbins 2001; Robbins 2007). However, more affiliative relationships may exist between related males or those who have coexisted for some time, which may in turn affect the dispersal patterns of maturing males (Harcourt 1979; Harcourt & Stewart 1981).

Other types of social relationships, such as interactions among silverbacks in multimale and all-male groups, have been examined as the composition of the study groups has permitted over time (Robbins 2001). In heterosexual groups, silverbacks may coexist for 10 or more years, with obvious dominance hierarchies (Robbins 1995; Robbins 2001). Despite this, relationships between silverbacks in these type of groups remain weak, with males spending little time in proximity with one another (<5 m), and rarely affiliating (Sicotte 1994; Robbins 1996). Rates of aggression depend on a number of factors, including age and relationship stability of males as well as number and reproductive status of existing females (Robbins 2001; Robbins 2007). Aggression can be either initiated or received by the silverback, as is also true for blackbacks (Robbins 2007). Agonistic interventions are also rarely observed among silverbacks (Robbins 1996; Watts 1997), though this may be due to the fact that most multimale groups include no more than two silverbacks. In addition, no reconciliation between males has been observed (in mountain gorillas) (Watts 1995).

Despite the low levels of affiliative relationships between males in heterosexual groups, those individuals with stable dominance relationships appear to, nonetheless, coexist predominantly through avoidance or tolerance, rather than frequent, high levels of aggression (Robbins 2007). In addition, Sicotte (1995) suggests that interpositioning by females and

infants between two competing males may be a proximate mechanism that facilitates male coexistence. Groups can even benefit from their multimale structure during intergroup encounters against extragroup males (Sicotte 1993; Robbins 2001; Watts 1989, 2000).

Although usurpation of the alpha male by younger silverbacks in multimale groups has been observed (Watts 1990; Sicotte 1993; Robbins 1996), these formerly dominant males may have been alpha in their group for 10 or more years. Robbins' (2007) observations of usurpation in Bwindi suggest that this process may be lengthy, comprised of several years of agonistic encounters, rather than a quick turnover. Afterwards, deposed males usually retain positive relationships with females, and they are not evicted from the group. Although allowing the deposed male to remain in the group may eventually lower the direct fitness of the dominant male (if the former sires offspring), the benefits of retaining a multimale group status may outweigh the costs (i.e. greater defense during intergroup encounters, reduced risk of infanticide) (Robbins 2007).

Relationships between males in *all*-male groups, however, are markedly different than those in heterosexual groups, possibly because the absence of females reduces competitive interactions (Yamagiwa 1987; Robbins 1996). Dominance relationships are still apparent between males of differing age classes, but these relationships are not as clear within age classes, especially among blackbacks (Robbins 2001; Robbins 2007). Though males in all-male groups exhibit higher rates of aggression compared to that of heterosexual groups, most of these conflicts are mild, consisting of mild pig-grunting or moderate displays as opposed to actual physical contact (Robbins 1996). This is exemplified by the fact that males exhibit more wounding in heterosexual groups (Robbins 1996). Interventions during aggressive encounters may also play an important part in sustaining group cohesion, with less

dominant males mediating in fights between older silverbacks in all-male groups (Yamagiwa 1987, 1992).

Affiliative interactions are also more common among males in all-male groups, where individuals engage in more grooming and playing compared to heterosexual groups (Robbins 2001; Robbins 2007). Sociosexual behavior is also observed, but at low rates (Robbins 2007). Despite the absence of reproductive opportunities, these all-male groups may provide maturing males with a better opportunity to expand on their developing social relationships, as opposed to becoming solitary males (Robbins 1996; Robbins 2001; Levrero et al. 2006). Being exposed to other males can allow individuals to gain experience in both aggressive and affiliative social interactions (Robbins 1996; Gatti et al. 2004), so that they may eventually emigrate to form their own successful group (Robbins 2001).

The benefits of all-male groups are also argued for captive western lowland gorillas (Stoinski et al. 2001; Pullen 2004; Stoinski et al. 2004a,b). This is due to the fact that, recently, this type of grouping has been observed in wild populations of this species (Gatti et al. 2004). Researchers suggest that all-male groups can be a functional social unit for maturing male gorillas in captivity. Stoinski and colleagues (2004) maintain that the best time to form these groups is when the males are still immature, as gorillas in this age class have been observed to form some of the most stable groups. In addition, effort should be made to diversify the groups in terms of rearing history (limiting, if possible, the amount of hand rearing experienced by males). Groups should contain no more than three or four individuals, and exhibits should be designed to provide visual barriers in order to provide refuge for subordinate males. Through these and other efforts it is hoped that all-male

(bachelor) groups can be a cohesive social unit for western lowland gorillas in captivity (Stoinski et al. 2001, 2004a,b), as has been shown for maturing mountain gorillas in the wild.

In conclusion, studies show that, in general, weak male-male relationships exist in mountain gorillas. However, younger, maturing males in all-male groups that have no reproductive opportunities to compete over (as well as no alternative social partners) have stronger relationships with each other than do males in heterosexual groups (Robbins 2001). The weak social relationships found among males in heterosexual groups suggest that competition over limited resources (females) is more influential than the benefits of cooperative defense of females from outsider males (Robbins 2001). This is exemplified by the fact that when an all-male group joined together with the females and offspring of a recently heterosexual one-male group (following the death of the silverback), the rates of aggression between two silverbacks (from the all-male group) increased considerably until one of the silverbacks was evicted from the group (Watts 1989).

Female-Male Social Relationships

Because both females and males benefit considerably from their interactions with one another, social relationships between the two sexes are said to be the foundation of gorilla societies (Harcourt 1979; Fossey 1983; Stewart & Harcourt 1987). Males benefit from having long-term access to females as a mating strategy, and females benefit from male protection against predators and infanticide (in mountain gorillas) by extra-group males (Wrangham 1986; Watts 1989; Robbins 2007). Specific female-male dyads may coinhabit a social group for more than 10 years (Robbins 2007), and these relationships can influence female transfer patterns (Watts 1992, 1996, 2003). If a multimale group fissions, such relationships may influence which male a female will choose to remain with (Robbins 2001;

Watts 2003). Therefore male behavior appears to be geared towards acquiring new mates, preventing the emigration of females, and protecting offspring (Robbins 2001).

In one-male groups females appear to be mainly responsible for maintaining social proximity (Harcourt 1979). Mountain gorilla groups spread out during feeding periods and then assemble near the silverback during resting sessions (Fossey & Harcourt 1977; Harcourt 1979). Females might spend as much as 50% of their resting time and around 20% of their feeding time within 5 meters of the silverback (Watts 1992). A captive study (Nakamichi & Kato 2001) also supports this phenomenon. Here, the silverback male in a one-male group was predominantly surrounded by five adult females, with some females maintaining proximity to the silverback male more frequently than others. This is in contrast to wild multimale groups, where males are mostly responsible for maintaining proximity to females when they are proceptive (Sicotte 1994).

The reproductive status of females is also thought to be an important factor influencing female proximity to males (Robbins 2001). In mountain gorillas, females with young infants spend significantly more time near silverbacks than do other females (Harcourt 1979; Robbins 2001). This is most likely to acquire protection from and familiarization with the silverback. However, this may not be the case for all species of gorillas or all types of social settings. One study of captive western lowland gorillas, by Stoinski and colleagues (2003), showed higher levels of proximity to juveniles and females by mothers during the six months after parturition. This is thought to reflect the lack of infanticide in captive gorillas, and perhaps indicates that these patterns may be representative of wild populations of western lowland gorillas as well (Stoinski et al. 2003).

Grooming, though a common signal of affiliation in most primates, is not a typical activity among mountain gorillas (Robbins 2001). However, when it does occur, grooming is most commonly observed between adult males and females (Robbins 2007). In these instances, though, it is not clear whether one sex gives or receives more grooming than the other (Harcourt 1979; Watts 1992). Some males, especially silverbacks in less dominant positions, may use grooming as an affiliative mating strategy (Watts 1992).

Silverback mountain gorillas are dominant over females, but females are often dominant over blackback males (Robbins 2001). Though it is not known at what age the rise in dominance occurs for males, it is assumed to correlate with the increase in size as males reach maturity (Robbins 2001). Though common (Stokes 2004; Robbins 2007), most aggression directed towards females is mild, consisting of pig-grunt vocalizations and displays (i.e. chest-beating), and only minimally results in physical injury (Watts 1992). The only submissive behavior observed in gorillas, grumbling, often occurs after females receive aggression from males, especially following displays (Watts 1994). In addition, males and females will usually engage in postconflict reconciliations with one another following an aggressive encounter (Watts 1995).

Though it is not fully understood why male gorillas frequently exhibit aggression towards females, it is thought to be attributed to the male's means of demonstrating his protective abilities to females (Robbins 2007; but see Harcourt 1979, Watts 1992, and Sicotte 2000 for aggression directed towards newly emigrating females). In addition, much of this aggression might be considered courtship aggression or sexual coercion. For example, Watts (1992) found that only a minority of the agonistic behavior exhibited by silverbacks towards females was in the context of feeding. In contrast, more than 60% might be classified as

courtship aggression, consisting of displays and interventions in sexual interactions. In addition, females' reproductive status also has an influence on levels of aggression, further emphasizing the role of courtship aggression (Watts 1992). In multimale groups, both dominant and subordinate males increase their rates of aggression toward females that are sexually active (Robbins 2003); however the silverbacks in one-male groups do not (Harcourt 1979).

Female Social Relationships

In general, female mountain gorillas have very weak social relationships with one another (Harcourt 1979; Stewart & Harcourt 1987; Watts 1994, 1995, 2001). This is in sharp contrast to the relationships observed in many other Old World anthropoid primate species, where the effects of relatedness are stronger and more consistent, and cooperation between non-relatives can even be important (Watts 2001). Due to these differences, female gorilla social relationships are classified as "non-female-bonded" (Wrangham 1979; van Schaik 1989) and "dispersed egalitarian" (Sterk et al. 1997). One major reason for this type of relationship lies in the fact that food resources are abundant and evenly distributed, which leads to very low levels of contest competition (Watts 1984, 1994), and competition for resources largely determines the social relationships found among female primates (Sterck et al. 1997; but see Pruetz 2009). With minimal benefits acquired from associating with other females, and low ecological and social costs from transferring to new habitats, female transfers into new groups can occur (Watts 1990). Therefore, females are typically seen in social groups containing unrelated individuals. However, mother-daughter and sister pairs are not uncommon because females may transfer together or even remain in their original groups (Watts 1996, 2001).

The fact that female relationships appear to be of little value in mountain gorillas is further emphasized by the very low to nonexistent rates of reconciliation following contests among females (Watts 1995). Although opponents sometimes engage in friendly interactions shortly after a conflict, rates of postconflict reconciliation are not consistently elevated compared to affiliation rates during 'control' samples or compared to baseline (Watts 1995).

Despite low levels of competition over food, aggression among gorilla females is most common while feeding (Robbins 2007). However, it may also occur during resting and traveling bouts when females are intolerant of being in close proximity to one another (Watts 1994). Intervention during aggression is most often by males as opposed to females (Watts 2001), and contests are ended without either, or any, opponent clearly losing (Watts 1997). Males' intervention in dyadic contests reduces the likelihood that aggressors direct multiple acts of aggression toward their opponents, and prevent prolonged sequences of aggression in which opponents would often have engaged in otherwise (Watts 1995). Therefore, it is assumed that male control of female aggression protects females and limits damaging aggression (Watts 1994, 1997). Given that females can easily transfer between groups with little ecological or social costs, this type of male intervention could possibly represent a mating strategy that reduces female emigration (Watts 1994, 1997).

While dominance hierarchies between male gorillas may prevent aggressive disputes, dominance relationships among females are often weak or nonexistent (Harcourt 1979; Harcourt & Stewart 1987, 1989; Watts 1985, 1994). However, a recent study suggests that female dominance hierarchies exist, and that they are even stable over time. Robbins and colleagues (2005) found female mountain gorilla linearity indices consistently greater than 0.95. They suggest that previous research may have reflected an insufficient quantity of data

for this species, rather than nonlinearity of hierarchies. They found that dominance depended on age and group tenure, as opposed to nepotism, with some females retaining a high rank for most of adulthood (15-25 years). Rank shifts most often occurred through changes in group composition, rather than switches in established relationships. Because of these findings, these authors propose that the dominance relationships of female mountain gorillas be categorized as "Dispersal-Individualistic" instead of "Dispersal-Egalitarian" (Robbins et al. 2005).

In contrast to the agonistic behaviors exhibited between females, affiliative interactions (particularly grooming and resting in close proximity) do occur at high rates among maternally related individuals, compared to those that are unrelated (Watts 1994). Grooming is often reciprocal among female dyads, but this is attributed to the high degree of grooming among relatives (Watts 1994). Overall, female relatives are said to have 'good' relationships with each other, engaging in higher levels of affiliative interactions and lower levels of aggression. Unrelated females are characterized as having 'bad' relationships, consisting of lower levels of affiliative interactions and higher levels of aggressive interactions (Watts 2001). However, in rare cases, unrelated females have 'good' relationships as well (Watts 2001).

The kin component can also be witnessed in female mountain gorilla coalitions. Watts (2001) found that most female coalitions occurred between relatives (especially maternal relatives, but also presumed paternal half-sisters), and that these usually involved support that one female gave to a relative who had initiated aggression against a non-relative. In addition, females with no female relatives present faced more oppositional female coalitions compared to females with relatives present. Maternal and some (presumed)

paternal relatives also exchanged support during agonism consistently and often enough to be considered allies. Watts (2001) observed a few non-relatives as allies, but states that most unrelated dyads did not support each other at all. Therefore, he concludes by suggesting that coalitions and alliances are absent in groups containing only unrelated females.

With the assumption that fruit is usually distributed in a clumped fashion, the increase in frugivory experienced by lowland gorilla populations is expected to lead to higher levels of within-group contest competition and differentiated female-female social relationships, including linear dominance relationships (Doran & McNeilage 1998, 2001; Scott & Lockard 2006). However, the limited number of habituated gorillas at these sites currently limits tests of this hypothesis to two locations (Robbins 2007). Although females in Bwindi Impenetrable National Park, Uganda, exhibited higher rates of aggression when foraging on fruit versus herbaceous vegetation, they did not differ overall in their relationships when compared to Karisoke mountain gorillas (Robbins, unpublished data). These female gorillas had a high degree of bidirectionality in aggression, low rates of affiliative behavior, and exhibited weak dominance relationships overall.

Observations of western gorillas at Mbeli Bai, Republic of Congo, also failed to show any noticeable differences in female social relationships, as compared to those of Karisoke (Stokes 2004). However, this study provided only a limited view of the females' social behavior because the gorillas were only observed feeding on abundant, evenly distributed aquatic vegetation, and the observations did not include any frugivorous behavior (Robbins 2007). Therefore, this study may not be representational of normal western gorilla daily activity (Magliocca et al. 1999; Parnell 2002). Detailed studies of habituated western

lowland gorillas are vital so that we may better understand the influence that frugivory has on gorilla female social relationships (Robbins 2007).

In conclusion, social relationships between female mountain gorillas are differentiated, with some dyads much more tolerant of each other and engaging in higher levels of affiliative interactions. Based on this, some females form coalitions, and some do this frequently enough to be considered allies (Watts 2001). Relatedness appears to have the strongest influence on relationships, with the effects of maternal relatedness more influential than others. From this, most non-relatives have few affiliative interactions, and many are also intolerant of each other. Agonistic relationships among females have been seen as both egalitarian and individualistic regarding dominance relationships, and males may often intervene in contests between females. In this way, male control of females is seen as a way to help males retain females. The advantages for females in choosing males that can effectively protect them against infanticide and other risks often outweigh the benefits of remaining with female relatives. Therefore female dispersal is not uncommon in mountain gorillas.

Conclusion

Across the animal kingdom there exists a wide variety of social systems (Robbins 2001). The degree of sociality and the type of social system exhibited by a species is influenced by many factors, especially those of ecology and behavior (Emlen & Oring 1997; Wrangham & Rubenstein 1986; van Hooff & van Schaik 1992; Lee 1994). These social systems are the result of individual strategies to maximize fitness, and both inter- and intraspecific variation can be seen (Robbins 2001). Examining the variation in social systems not only improves our understanding of the proximate mechanisms that produce

such variation, but also heightens our awareness of the adaptive significance of sociality and the evolution of social structure (Lott 1991). Because behavioral ecologists are no longer labeling species as static in their patterns of behavior and social structure, we now examine such influential variables as group size, age structure, sex ratio, degree of relatedness, and others in the species that we study (Strier 1994).

Because primates exhibit such diversity in their social systems (Smuts et al. 1987), they provide us with a unique opportunity to examine the resulting effects of both ecological and behavioral variables among species. More specifically, studies of various gorilla species provide us with the chance to reevaluate proposed models of ecological influence on social organizations found within African great apes (Doran & McNeilage 2001). Because western lowland and mountain gorillas differ extensively in their habitat, resource availability, and foraging strategies (Doran & McNeilage 2001), they allow us to assess just how these distinctions affect the social organization of gorillas, a genus comprised of multiple unique species that were once viewed as virtually the same.

2.2 A Closer Look at Wild Male Gorillas

Group Structure

In most gorilla populations, both male and female gorillas emigrate from their natal group before reaching adulthood. However, unlike females, males rarely join breeding groups. Instead, these younger gorillas usually wander alone as solitary individuals, join all-male groups, or are joined by females to eventually become a one-male group (Harcourt & Stewart 1987). Leaving their group as blackbacks or young silverbacks, then, helps to explain why most gorilla groups have only one fully adult male. Though emigration is most

common, some males will remain in the group they were born in, thus forming the alternative multi-male group. Various factors determine the type of group structure that a male will reside in, and these are discussed in the following sections.

Solitary Males

Solitary males are usually those gorillas that emigrated from their natal groups before they have bred, to travel alone. Though they most likely will not remain solitary, it may still be many years before these males can permanently attract females to their 'group'. Male gorillas acquire females by attracting them away from other silverbacks during encounters with heterosexual (one-male or multi-male) groups. These encounters may involve intense male-male competition, with conflicts involving either displays, or actual physical fighting (Harcourt & Stewart 1978). In fact, it is even thought that this intense competition (among males for females) has contributed to the gorilla's extreme sexual dimorphism, with females weighing only about half that of males (Harcourt & Stewart 2007). Males, in contrast to females, also possess a number of morphological features associated with an ability to fight (such as the secondary sexual characteristics previously described), and thus are subsequently better able to protect their group, and retain those females. Solitary males, then, may also be the result of a male whose females deserted him, though this is not nearly as common (Watts 2000).

Rather than form their own social group, solitary males may also join nonreproductive groups (Robbins et al. 2004). However, their residence in these 'bachelor' groups will only be temporary until the once solitary blackback has matured. He will then move on to eventually acquire his 'own' females. Though males are not solitary permanently, their existence can still be readily observed in the wild. In a seventeen month

study, Gatti and colleagues (2004) observed a total of 377 gorillas. Eight percent of these were solitary males, and 44% of the blackbacks that were observed were solitary individuals, suggesting that this temporary 'group' structure is not at all uncommon for sub-adults.

One-male groups

Though residing temporarily as solitary males may be relatively common, living in one-male groups is even more common for wild gorillas. Over 95% of western and eastern lowland gorilla groups are one-male groups (Harcourt & Stewart 2007). The less numerous mountain gorillas, in contrast, are characterized as having approximately 41% one-male groups. These high percentages mean that over 94% of all gorillas in the wild reside in one-male groups. It has also been calculated, by Harcourt and Stewart (2007), that 97% of all gorilla *breeding* groups have only one fully adult male.

These social groups form, as previously mentioned, when females transfer from their natal or subsequent breeding group to a lone silverback (Robbins 2007; Parnell 2002, Harcourt & Stewart 2007), or in rare cases, when a multi-male group splits permanently into two units, each with its own silverback (Parnell 2002). Such groups typically remain one-male until male offspring mature into silverbacks. These one-male groups will subsequently become multi-male groups if the maturing male offspring do not emigrate out of the group (Robbins 2007).

Multi-male groups

A third gorilla group type, multi-male, consists of two or more silverbacks, females, and young of either sex. Because males rarely emigrate into heterosexual groups, it can generally be assumed that their formation is based on within group parameters. For example, multi-male groups usually consist of either father-son or brother/half-brother combinations

(Robbins 2001). These same mature males may coexist for periods of over 10 years, indicating that multimale groups are not temporary situations. In fact, in studies by Robbins (1995) and Watts (2000), less than half of all males that reached maturity in heterosexual groups emigrated. This is in contrast to males found in all-male gorilla groups, where all males eventually emigrated.

Although the majority of gorilla groups are one-male, the multi-male group can provide a number of advantages to the individuals within them, compared to one-male groups. For example, in multi-male groups there is a reduced risk of infanticide, and immature males have an increased likelihood of remaining in a heterosexual group through maturity compared to individuals growing up in a one-male group (Robbins 1995). If the silverback in the latter group type dies, the females move into other groups in which the new silverback is typically intolerant of offspring sired by another male, leading to infanticide of unweaned infants (in mountain gorillas) (Watts 1995). Immature males may then face group eviction and may end up in all-male groups. However, if a silverback in a multi-male group dies, another silverback is often able to take over leadership and retain a stable group setting (Robbins 2005).

The benefits of multi-male groups continue into adulthood as well. Males that adopt the strategy of staying within their natal group when they reach maturity appear to have a higher success rate in terms of obtaining reproductive opportunities, compared to males who disperse and attempt to form new groups (Robbins 1995; Watts 2000). Additionally, coalitions of males may serve to prevent female emigration during inter-group encounters (Robbins 2001). Finally, if a silverback loses his dominance status as he ages, he will still be

allowed to remain within the group (Robbins 2005). This is also beneficial because these males can provide further protection and care to their offspring.

The many benefits of multi-male groups beg the question of why they are not more common. Harcourt and Stewart (2007) suggest that this may be because many males simply do not have the choice to stay within their natal groups. For example, if a group disintegrates after the breeding male has died (as mentioned previously), the maturing males cannot immigrate into breeding groups as females can, and become 'leavers' by default. In addition, if the male faces high levels of mating competition with a dominant silverback still in his prime, it may be worthwhile for that male to move elsewhere. But aside from becoming a solitary individual, where might these maturing males go?

All-male groups

All-male groups may form through a merger of immature males and a solitary silverback (Robbins 2005; Gatti et al. 2004). Alternatively, all-male, or nonreproductive groups, may also form by default after females have deserted their 'original' heterosexual group (Robbins 2004). Despite frequent changes in members due to male migrations, these all-male groups persist, indicating that they may play an important role in the life of maturing migrating males (Gatti et al. 2004).

As previously mentioned, relationships between males in all-male groups are markedly different from those in heterosexual groups (Robbins 2007). This is assumed to be the result of a decrease in competition due to the absence of females in the group. Dominance relationships are still evident, however, but they may be less clear within age classes, especially with blackbacks. Rates of aggression are higher than in heterosexual groups, but most of these conflicts consist of vocalizations and displays, with lower instances

of actual wounding. Males also exhibit higher rates of grooming and playing, and spend more time in close proximity with each other, compared to males in heterosexual groups.

Despite the lack of reproductive opportunities, all-male groups may be a better alternative for maturing gorilla males because the social setting they provide allows these males to gain experience in aggressive and affiliative interactions (Gatti et al. 2004). However, the fact that these all-male groups rarely consist of more than one silverback at a time should suggest that all-male groups in captivity will not form a long-term solution to the problem of 'surplus' males. In fact, Robbins (1995) states that mature males appear to benefit little from being members of all-male groups. This is because solitary adult males do not join (already formed) all-male groups and because males leave these groups at maturity to become solitary (Harcourt & Stewart 2007).

Social Structure

Having looked more closely at male gorilla *group* structures, it is now more feasible to examine the specific *social* structures of males found within the various group types. The following section examines three male (age-related) relationships found in gorilla societies: immature relationships (consisting of juveniles, subadults and blackbacks), immature-silverback relationships, and silverback relationships.

Immature Relationships

Social interactions among immature gorillas occur at a higher frequency, compared to interactions among adults, in both wild and captive populations (Stewart & Harcourt 1987; Stoinski et al. 2004). The most common type of interaction is play. Play likely serves as one of the most important behaviors for the development of social skills in gorillas (Robbins

2007). Play typically begins around nine months of age, peaks during the juvenile stage, and then decreases during adolescence. Grooming also occurs between immatures, with older individuals grooming more often than younger ones. There is evidence to suggest that maternal siblings groom each other preferentially as well (Harcourt & Stewart 1987). Among immatures, dominance rank is positively related to age and is not dependent on sex or maternal rank. After puberty, however, sex differences become apparent, and as males grow larger in size, they begin to dominate females in aggressive interactions, and then eventually even outrank adult females.

Immature-Adult Relationships

A silverback's primary contribution to infant gorillas (at least in mountain gorilla societies) is for protection against infanticide from unrelated, extragroup males (Watts 1989). Therefore, a silverback should be more affiliative toward offspring that he sired, compared to unrelated infants in his group, as has been exemplified in a captive study of western lowland gorillas (Enciso et al. 1999). Here, significantly higher degrees of affiliation and tolerance occurred within the silverback-offspring dyad, compared to the dyad consisting of a silverback and an unrelated infant. Furthermore, the unrelated infant was the recipient of over 40 percent of the agonistic behaviors exhibited by the silverback, while no such encounters were recorded within the related dyad.

There are many other benefits to immature-silverback associations, aside from infanticide-avoidance. As a gorilla reaches late infancy, it increases the amount of time it spends in close proximity to the silverback. In fact, immature gorillas are attracted to the silverback as the focal point of the group and spend significant time near him, even when their mothers are not nearby (Robbins 2007). Silverbacks also intervene in aggressive

encounters between immatures, and usually support the younger opponent. This, then, serves to protect immatures from aggression from older individuals (Harcourt & Stewart 1987). Indeed, silverbacks may even increase affiliative behaviors toward young that have lost their mothers through death or dispersal, including grooming and co-nesting with them.

Silverback-blackback relationships, on the other hand, are much weaker. This is based on low levels of proximity and affiliation, as well as unidirectional aggression from the silverback to the blackback (Robbins 2007). Silverbacks are always dominant over blackbacks, who themselves spend a considerable amount of time on the periphery of the group (perhaps to avoid conflict with the silverback or adult females). However, more affiliative interactions may occur between those males that are related, or those who are more familiar with each other (Robbins 2007).

Adult Relationships

Social groups that contain at least two adult silverbacks may exist for more than ten years, as is seen in mountain gorillas (Robbins 1995). Among these males, dominance hierarchies are obvious, but age is not always the determination of rank. These silverbacks spend little time in close proximity (<5 meters) with one another, and rarely affiliate. Rates of aggression between males in these groups depend on a number of factors (Robbins 2007). For example, conflict severity and frequency can be determined by the number and reproductive status of females, the age of the males, and the stability of their relationships. Aggression may intensify when females are sexually active, but this is not always the case (Robbins 2003). In some instances, dominant males increase aggression toward subordinates, while in other cases the opposite is true. Both dominant and subordinate males

may harass each other during mating, but dominant males are more successful in stopping copulations than subordinates are (Robbins 1999).

In multi-male gorilla groups, conflicts between silverbacks sometimes induce infants and females to interpose between the opponents (Sicotte 1996). In these instances, aggressive interactions between individuals can be disruptive for females and their young, preventing them from feeding and resting normally. Therefore, as a mechanism for resolving conflict among silverbacks, interpositions serve to reduce the rate of aggression between males. Likewise, these interpositions might also be one of the important mechanisms allowing adult male coexistence in gorillas.

Reconciliation between adult males has not been observed in mountain gorillas (Watts 1995). Robbins (2007) suggests that this is due to the fact that when males have stable dominance relationships they appear to coexist predominantly by avoidance and tolerance. This is in contrast to alternative relationships, which might suffer frequent, high levels of aggression.

Dominant silverbacks may remain in charge of their group for ten or more years. Usurpation of the alpha silverback by younger silverbacks may involve a lengthy process (several years) of agonistic encounters, as apposed to a quick turnover. Deposed males are usually not evicted from heterosexual groups, and they typically retain positive relationships with adult females. However, if these males sire offspring and reduce the direct fitness of the new dominant male in the group, then why might they be allowed to stay in the group? Robbins (2007) suggests that eviction may be costly to the dominant male, and/or the benefits of retaining a multi-male status may outweigh the costs. These advantages include:

a more attractive group for females to join and remain in, reduced risk of infanticide, and additional defense (by coalitions) during extra-group encounters.

Conclusion

As has been illustrated, male gorillas can be found in a variety of group settings. These range from temporary solitary males to group living. Group structure incorporates either one (one-male groups) or multiple adult males (multi-male groups) within each heterosexual group; though the former is a much more common scenario in the wild. All-male groups may also be an option for maturing males. These groups provide a seemingly 'healthier' alternative to living solitary but are only temporary. This is due to the fact that adult solitary males do not join these groups, and because those males that reach adulthood within them generally leave the group. Male gorilla relationships range from frequent playfulness (among immatures) to avoidance and aggression (among adult silverbacks), and depend largely on age.

CHAPTER 3. METHODS

3.1 Subjects, Study Site and Data Collection

My research was carried out at the Henry Doorly Zoo in Omaha, Nebraska. Currently the zoo houses 14 gorillas in a variety of zoo enclosures. Subjects in my study included 9 male western lowland gorillas (Table 3.1). These individuals were housed in 3 separate outdoor enclosures during observations, which resulted in a total of 10 male-male dyadic relationships (Table 3.2). My observations were conducted during weekday zoo hours when these individuals were housed above ground in outdoor zoo exhibits (as opposed to smaller underground, indoor enclosures where they were housed at night).

Name	Age
Group 1	
Gerry	14
Ktembe	10
Group 2	
Tambo	13
Samson	12
Timmy	10
Group 3	
Motuba	22
Ngoma	13
Kijito	12
Tatu	8

Table 3.1 Table showing subject name, group number, and age during time of study.

My study was conducted from 4 June to 10 August in 2007 for a total of 10 weeks. I collected behavioral observations 5 days a week during zoo hours of operation (1000-1700 h) using the focal-animal sampling method with instantaneous recording (Altmann 1974) of a number of affiliative and aggressive social behaviors, along with general activity, every 30 seconds (see Appendix). I conducted 30 minute observational samples on each of the 9

gorilla subjects at predetermined times, so as to control for time of day and seasonal effects, using a digital stopwatch.

Dyad	Group #
Gerry-Ktembe	1
Tambo-Samson	2
Tambo-Timmy	2
Samson-Timmy	2
Motuba-Ngoma	3
Motuba-Kijito	3
Motuba-Tatu	3
Ngoma-Kijito	3
Ngoma-Tatu	3
Kijito-Tatu	3

Table 3.2 The 10 dyads (relationship consisting of two individuals) examined in this study

I recorded affiliative, aggressive, self-directed and general activity behaviors during observation sessions (see Appendix). Affiliative behaviors included grooming, playing, embracing, tolerated physical contact (Watts 1995a), and proximity (Mallavarapu et al. 2006). Specifically, I noted proximity when individuals were within 1, 2, and 5 meters of each other. One meter is generally used as a proximity measurement in various primate studies (Cords 1993). Two meters was used in order to represent a head and body length measurement of the adult male western lowland gorilla, which equals approximately 1.7 meters (Harcourt 1985). A 5 meter measurement has also been used when determining gorilla proximity (Watts 2001), and therefore was noted in my study as well. Aggressive behaviors were represented by chest beating, postural displays, lunging, hitting, kicking, shoving, chasing (not in play) and fighting (where individuals grapple and try to inflict wounds) (Lockard & Goyal in press; Watts 1995a).

In the event of a conflict, I collected continuous focal-animal (Altmann 1974) postconflict (PC) observations on one of the two individuals involved for a total of 30

minutes directly following the conflict. However, if that subject went out of sight, my observations continued on the other individual involved in the conflict. This was in order to note the first affiliation between the two former opponents. At the same time on the following 1 to 4 days I conducted a 30-minute matched control (MC) observation session (also continuous focal animal sampling). This was in place of the pre-scheduled observation session for that time. My observation schedule was then adjusted accordingly to continue to allow for equal observation of each individual.

These methods follow de Waal and Yoshihara's (1983) PC-matched controlled (MC) method most often used in postconflict observations. However, there are a number of variables that can alter these methods that should be noted. If, during PC or MC, both opponents were out of sight of the observer (due to barriers in the enclosure), the observation was not included in the analysis. Additionally, in a 'normal' session, if subjects did not engage in further aggression during the PC, focal animal sampling ended after 30 minutes. If, however, subjects engaged in a second aggressive encounter before the end of the 30 minutes, the 30-minute PC session started immediately after the termination of the second conflict. Additionally, if an agonistic encounter occurred between one or more of the opponents during the 30-minute MC period, the MC observation was cancelled and rescheduled for the following day.

3.2 Analysis

I compiled data to include the frequency of social interactions, general activity levels, and the duration of behaviors of opponents during PC and MC periods. I analyzed my data regarding postconflict and conflict variables (Table 3.3) using an Analysis of Variance test

(ANOVA), and results are represented in a number of scatter plots. Postconflict analysis followed the PC-matched controlled (MC) method (de Waal & Yoshihara 1983) where the timing of the first affiliative interaction between the two opponents during the PC and the MC periods were compared. For example, if the first 'friendly' interaction occurs only within the PC, or earlier in the PC than the MC, then the PC-MC pair is classified as "attracted". If the interaction occurs earlier in the MC than the PC, or only in the MC, then the PC-MC pair is classified as "dispersed". Consequently, if there are no affiliative interactions in either the PC or the MC (or if their timing is the same) the pair is considered "neutral".

Questions	Variables Examined
1. Do affiliative interactions between former (male gorilla) opponents occur sooner after a conflict than compared to matched control periods?	1. Time duration from the start of PC and MC periods until the first affiliative interaction.
2. Is more time devoted to affiliative interactions between former opponents in postconflict periods compared to that of matched control periods?	2. Total duration and frequency of affiliative social interactions in PC periods compared to MC periods
3. If postconflict reconciliations are evident among male gorillas, do they exist in the context of other behaviors besides proximity?	3. Duration and frequency of each type of affiliative social interaction during PC and MC periods.
4. Does group size influence the rate of postconflict reconciliation in male gorillas?	4. Total duration and frequency of reconciliation for each of the three (different sized) groups.
5. Does age influence postconflict behavior in male gorillas?	5. Total duration and frequency of reconciliation for each (different aged) individual.
6. Do subjects that exhibit more affiliative social behaviors overall engage in higher rates of postconflict reconciliation per conflict?	6. Total duration and frequency of affiliative social interactions for each individual compared to percentages of conflicts reconciled overall.
7. Do subject that exhibit more agonistic social behaviors overall engage in lower rates of postconflict reconciliation?	7. Total duration and frequency of agonistic social interactions for each individual compared to percentage of conflicts reconciled overall.
8. Does the age of the individual effect the number of conflicts an individual engages in?	8. Number of conflicts engaged in for each individual compared to age.
9. Does the age of the individual effect affiliative social interactions?	9. Total duration of affiliative social interactions for each individual compared to age.

Table 3.3 Table with questions analyzed and variables examined.

To analyze reconciliation, the total number of attracted and dispersed pairs compiled for all subjects is compared using a chi-square test, testing against a 1:1 expectation (Aureli et al. 1989). To analyze individual reconciliation, the Wilcoxon signed-ranks test is used to determine and compare the number of attracted and dispersed pairs for each individual animal. Data are also analyzed using the time-rule method (Aureli et al. 1989) to compare the timing of first affiliative interactions in the PC and MC periods. A Kolmogorov-Smirnov two-sample test (Veenema 2000) is used to establish a difference in time distributions between the two periods. Reconciliation data is then quantified by calculating the corrected conciliatory tendency (CCT) (Veenema et al. 1994), which is defined as follows: CCT = (number of attracted pairs – number of dispersed pairs)/total number of pairs.

CHAPTER 4. RESULTS

I did not run statistical analyses on post-conflict reconciliation due to the fact that I observed no reconciliation in dyads that were involved in conflict. In fact, opponents avoided one another, as much as their enclosure allowed, following conflict. A summary of the 45 conflicts observed in this study are presented in Table 4.1. These results show that approximately one-third of conflicts were display only, while another (approximate) third resulted in physical contact between the two opponents. The remaining conflicts (and also the majority) were chases, where the male being chased escaped before contact could be made.

	Chest Beat	**Display Posture**	**Chase**	**Shove**	**Hit**	**Fight**	**Display Only**	**Contact**
Frequency	6	8	19	1	3	8	14	12
% of Conflicts	13	18	42	2	7	18	31	27

Table 4.1 Frequency and percentage of conflict type. "Display Only" represents both "Chest Beat" and "Display Posture", while "Contact" represents "Shove", "Hit" and "Fight".

Understanding the prevalence of various social and nonsocial behaviors is important when examining the quality of life for captive primates. For this reason, I also investigated general activity levels, in addition to conflict-related data. Before I begin data analyses, however, it is important that I note a possible limitation of the study. Due to a sample size of 9 individuals, results may be more suggestive than definitive, and randomness is assumed to generalize to a larger population.

My results will be assessed first at the individual level, followed by analyses at the dyadic level. Though the former may appear most appropriate for study, the latter is actually

more essential for understanding various social behaviors, since sociality cannot occur at the individual level. However, I statistically analyze individual data in order to supplement dyadic data and help elucidate patterns seen in dyadic interactions.

I analyzed individual data through Analysis of Variance (ANOVA) tests comparing conflict with age, affiliation, and inactivity. I also analyze age and inactivity. My dyadic data were analyzed with ANOVA tests as well. Here, I examine conflict and affiliation according to age.

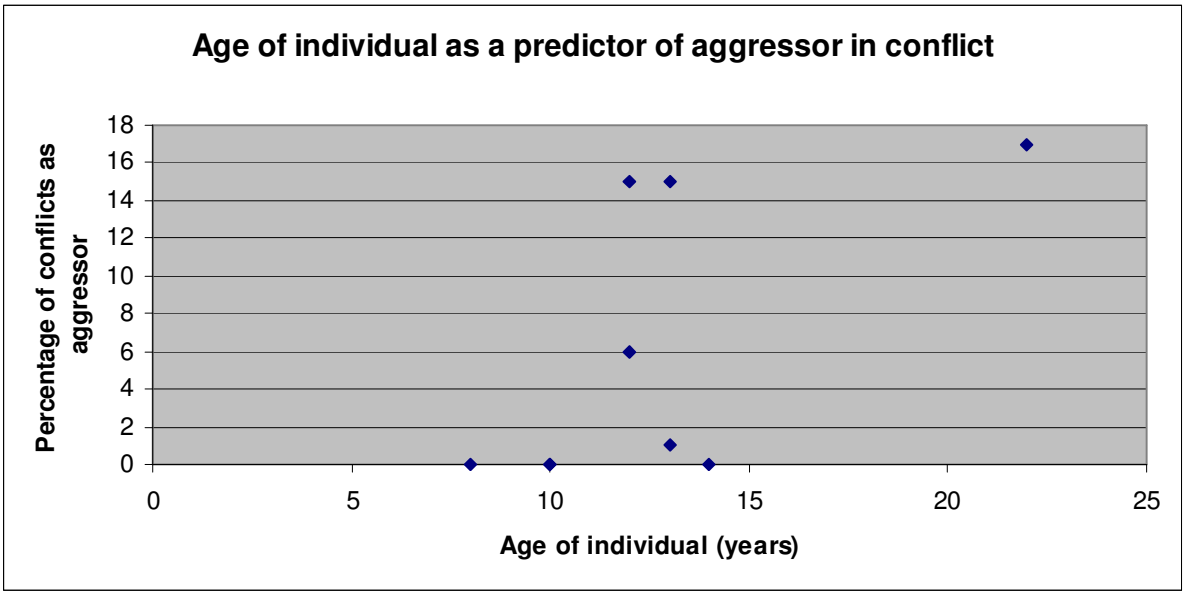

Figure 4.1 Scatter plot of age of individual and the percentage of conflicts (out of the total 45 for the population) in which that individual was the 'aggressor'. Slope=1.191; p=0.035.

4.1 Results on Individuals

Age and Conflict

I have reported raw data on individuals at the end of this section in Table 4.2. The age of subjects ranged from 8 to 22 years, the percentage of conflicts an individual initiated ranged from 0 to 17, and the percentage of conflicts an individual was involved in ranged

from 0 to 23 (out of the 45 conflicts total). The percentage of conflicts an individual initiated was positively related to his age (Figure 4.1; slope=1.191; p=0.035). These results yield a lower p-value than an analysis of age and the number of conflicts an individual *engaged* in overall (slope=1.286; p=0.083).

Affiliation and Conflict

The percentage of hours individuals spent in affiliative interactions ranged from 0 to 6. The percentage of time that an individual spent in positive social interactions was negatively related to the percentage of conflicts in which the individual engaged in (slope= -3.325; p=0.012).

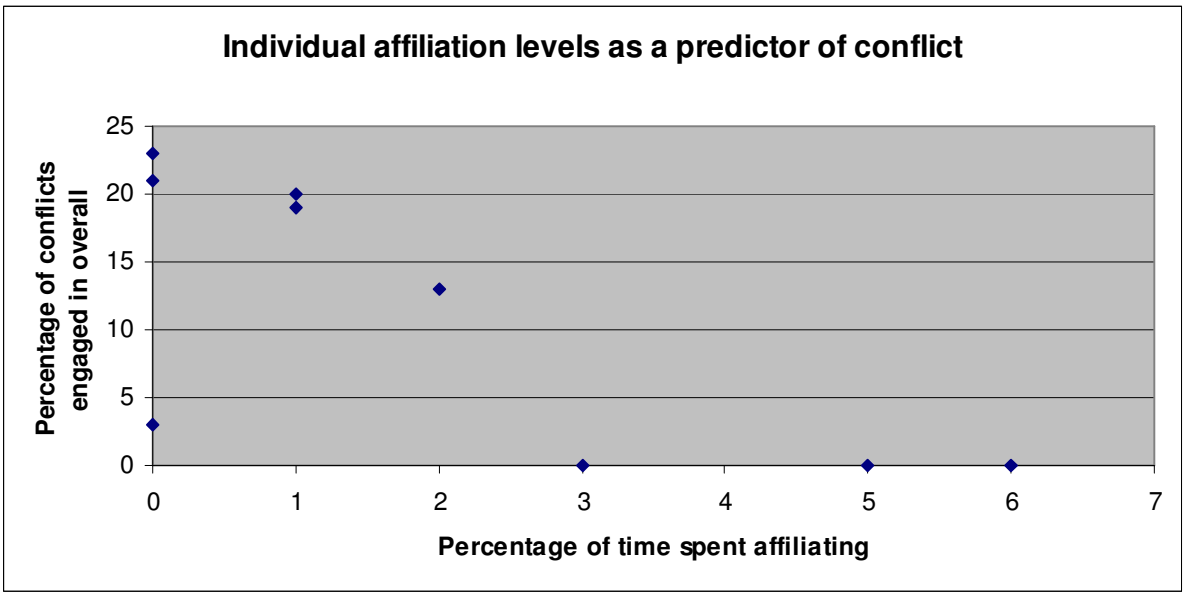

Figure 4.2 Scatter plot of individual affiliation levels and percentage of conflicts engaged in (out of the total 45 for the population). Slope= -3.325; p=0.012. Results show a negative linear relationship.

Inactivity, Age, and Conflict

Individuals were inactive 80 to 96 percent of the time. The more inactive an individual, the more likely that individual was to be involved in conflict (Figure 4.3; slope=

1.492; p-value= 0.0007). However, inactivity increased significantly with age (Figure 4.4; slope= 0.939; p-value= 0.038). Therefore, it is possible that age, rather than inactivity, explains the increase in conflict.

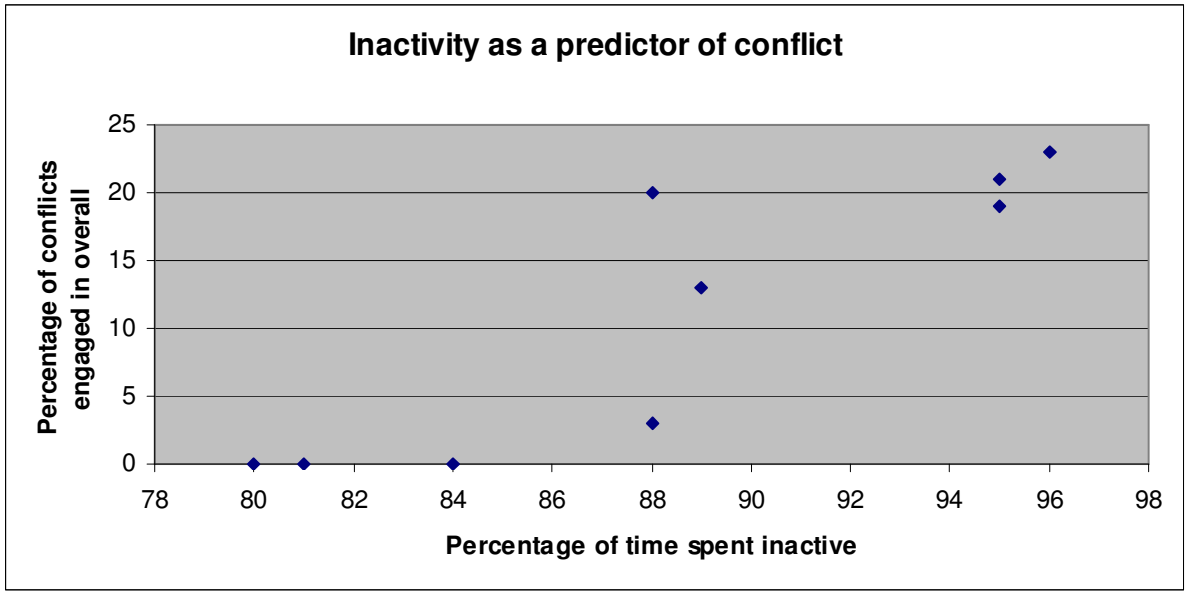

Figure 4.3 Scatter plot showing a positive linear relationship between conflict and inactivity. Slope=1.492; p= 0.0007.

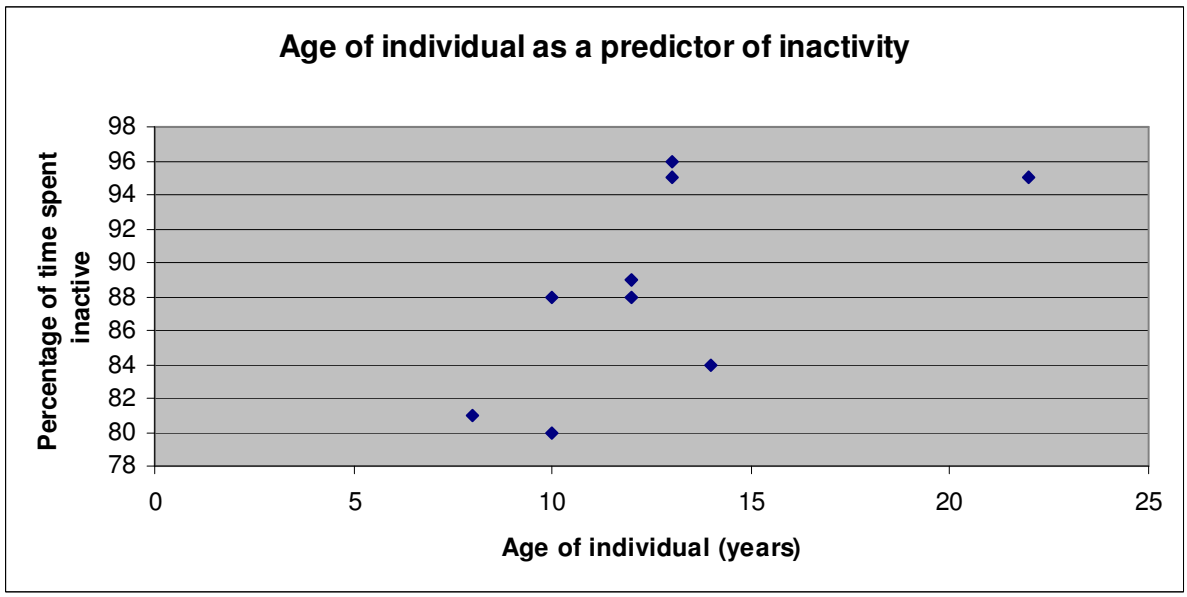

Figure 4.4 Scatter plot showing age as a predictor of daylight zoo hours spent inactive. A positive linear relationship is seen (slope=0.939; p=0.038).

Raw Data for Individuals

Subject	# Group	Age	# Aggsr	# Victim	% Conflict	% Inactive	% Social	% Scl+Pr	% Travel
Gerry	1	14	0	0	0	84	3	8	11
Ktembe	1	10	0	0	0	80	5	12	6
Tambo	2	13	15	6	23	96	0	1	4
Samson	2	12	15	3	20	88	1	10	7
Timmy	2	10	0	3	3	88	0	7	9
Motuba	3	22	17	0	19	95	1	38	2
Ngoma	3	13	1	18	21	95	0	0	2
Kijito	3	12	6	6	13	89	2	14	9
Tatu	3	8	0	0	0	81	6	51	10

Table 4.2 Individual data on the nine male gorillas in this study. Cream colored cells represent coded data; red indicates ranges of values. See following descriptions for heading explanations.

Subject: Names of each of the nine subjects
 # Group: Group membership of each individual in one of three groups
Age: Maximum age, in years, of gorilla during three month study
 # Aggsr: The number of times an individual was an aggressor of a conflict
 # Victim: The number of times an individual was aggressed upon in conflict
% Conflict: The percentage of conflicts each gorilla was involved in (out of the 45 conflicts total)
% Inactive: The percentage of time an individual spent resting/inactive, during daylight zoo hours
% Social: The percentage of time an individual spent in affiliative behavior, during daylight zoo hours
% Scl+Pr: The percentage of time an individual spent in affiliative behaviors, during daylight zoo hours, including proximity (within 5 meters)
%Travel: The percentage of time an individual spent traveling, during daylight zoo hours

4.2 Results on Dyads

I report raw data for dyads (interactions between two individuals) at the end of this section (Table 4.3). There were a total of 10 dyads in this study: one in group #1, three in group #2, and six in group #3. When my analyses used the age of the *youngest* subject in the dyad, results were significant (while using the age of the oldest individual in the dyad produced no significant results). Therefore, only the age of the youngest individual within each dyad influenced the social interactions of that relationship.

Age of Youngest in Dyad and Affiliation

Data on all dyadic positive social interactions (including proximity) range from 0 to 37 percent (in other words, dyads spent anywhere from 0 to 37 percent of the time affiliating with one another). The age of the youngest male in each of the 10 separate dyads ranged from 8 to 13 years. As the age of the youngest individual within a dyad increases, the level of affiliation within that dyad decreases (Figure 4.5; slope= -4.872; p= 0.017).

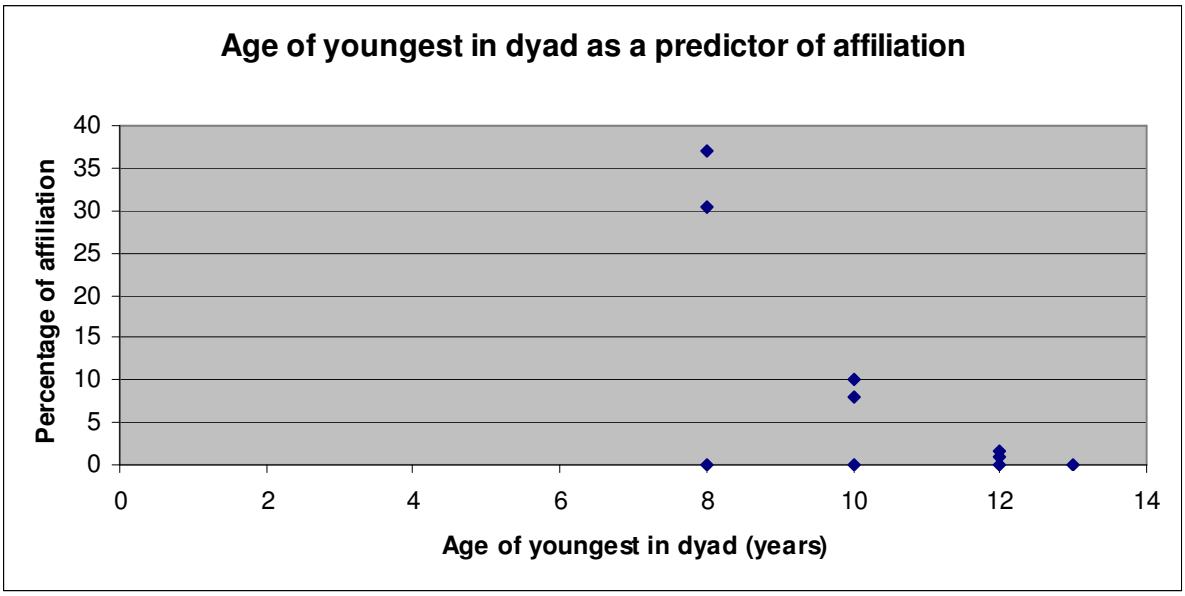

Figure 4.5 Scatter plot showing a significant linear relationship between the age of the youngest individual in a dyad and the levels of affiliation within that dyad (the percentage of time each dyad spent affiliating) (slope= -4.872; p=0.017).

Dyads with the youngest individual over the age of 11 averaged less than 1 percent of their time spent in affiliation with one another (0.625%). This is in sharp contrast to dyads where the youngest individual was *less* than 11 years old. Here, the average amount of time the dyad spent in affiliative behavior was over 14 percent (Figure 4.6).

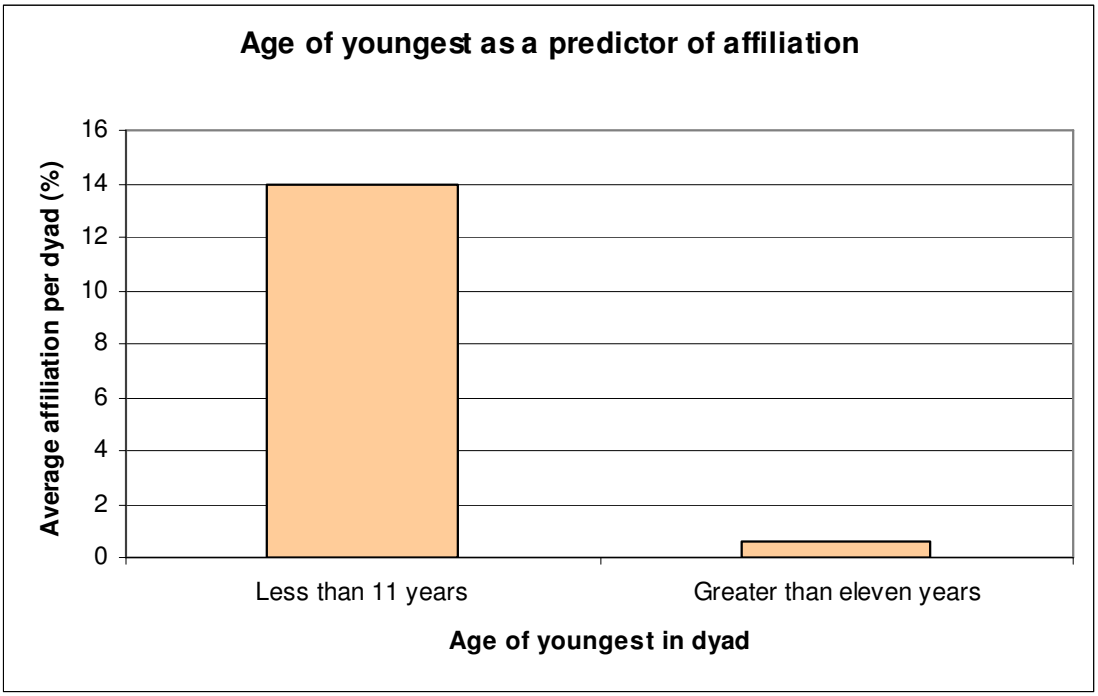

Figure 4.6 Bar graph illustrating the contrast in average affiliation between dyads where the youngest individual was less than 11 years old (>14%), and dyads where the youngest individual was greater than 11 years old (<1%).

Age of Youngest in Dyad and Conflict

Conflicts within each dyad ranged from 0 to 42 percent (of the 45 total conflicts). As the age of the youngest individual within a dyad increases, the number of conflicts increase (in contrast with affiliation, as reported above) (Figure 4.7; slope= 5.785; p=0.005).

Dyads where the youngest individual is over 11 years of age average 24% of conflicts (per dyad). This is in sharp contrast to those dyads where the youngest individual is *less* than 11 years of age, which average only 1% of conflicts (Figure 4.8).

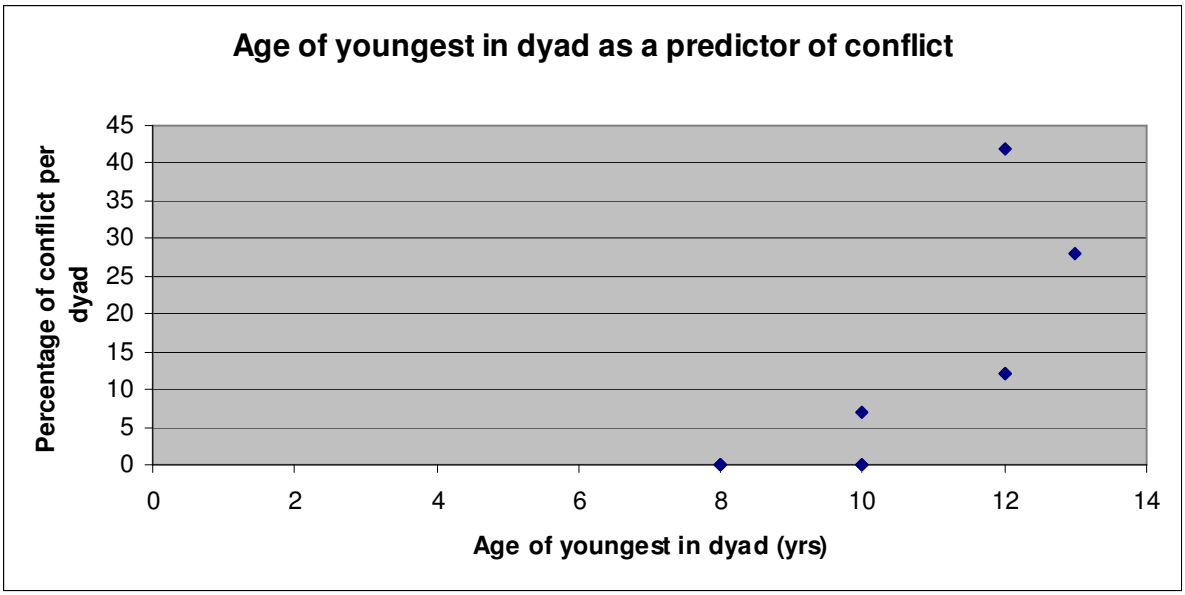

Figure 4.7 Scatter plot showing that as the age of the youngest in a dyad increases, the percentage of conflicts (out of the 45 conflicts total) increase as well (slope=5.785; p=0.005).

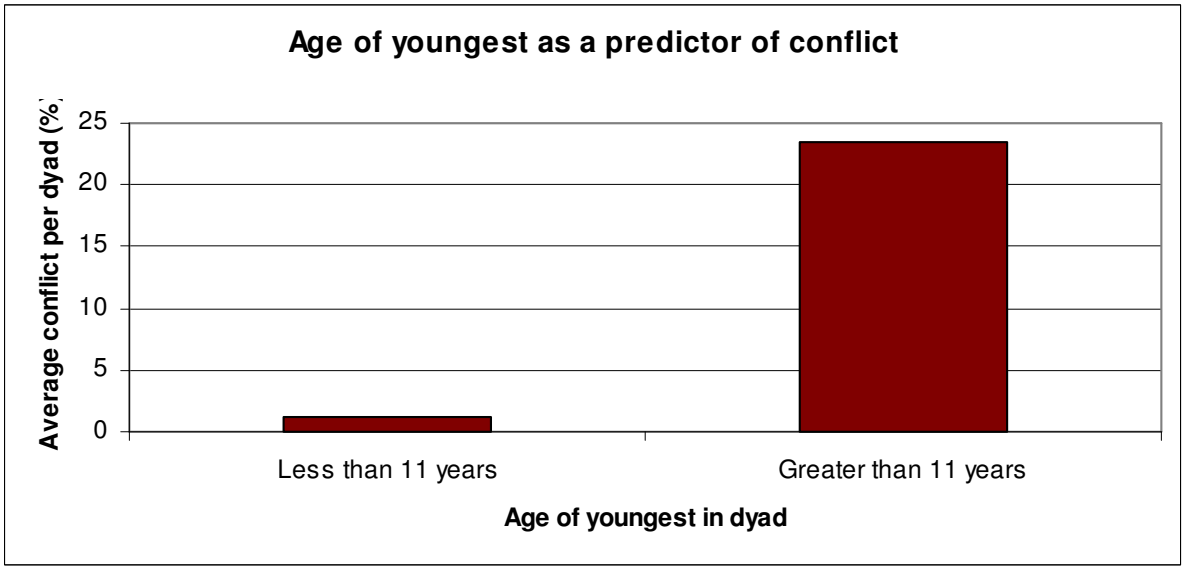

Figure 4.8 Bar graph contrasting average conflict levels between dyads where the youngest individual is less than 11 years of age (1%), and those where the youngest is over 11 years (24%).

Conflict and Affiliation

As the age of the youngest individual in a dyad increases, conflict significantly increases, and affiliation significantly decreases. Therefore an analysis of affiliation and conflict should result in a negative linear relationship, as can be seen in the following figure (Figure 4.9; slope= -4.248; p-value= 0.093).

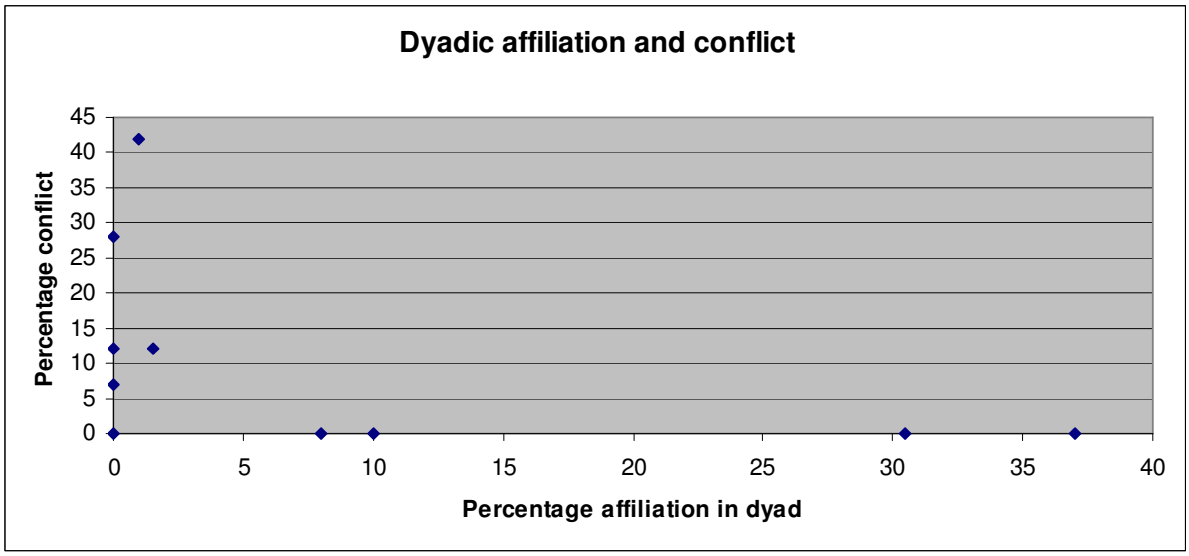

Figure 4.9 Scatter plot illustrating that where there is substantial affiliation, there is no evidence of conflict. Also that where there is conflict, there is almost no affiliation. These results illustrate all-or-nothing relationships for the case of affiliation and conflict. ANOVA test yields significant linear results at the 0.100 level (p=0.093).

What might be even more essential to the study, however, is not the linear relationship shown above, but is illustrated by the raw data (Table 4.3) and Figure (4.10) on the following page. Here it is important to note that those relationships with higher affiliative values (8%-37% of their time spent affiliating with one another), have absolutely zero conflicts. In addition, those relationships that consisted of conflict (7%-42%), have virtually no affiliation (0%-1.5%). There appears to be an all-or-none situation with most dyads consisting of either conflict or affiliation but hardly both.

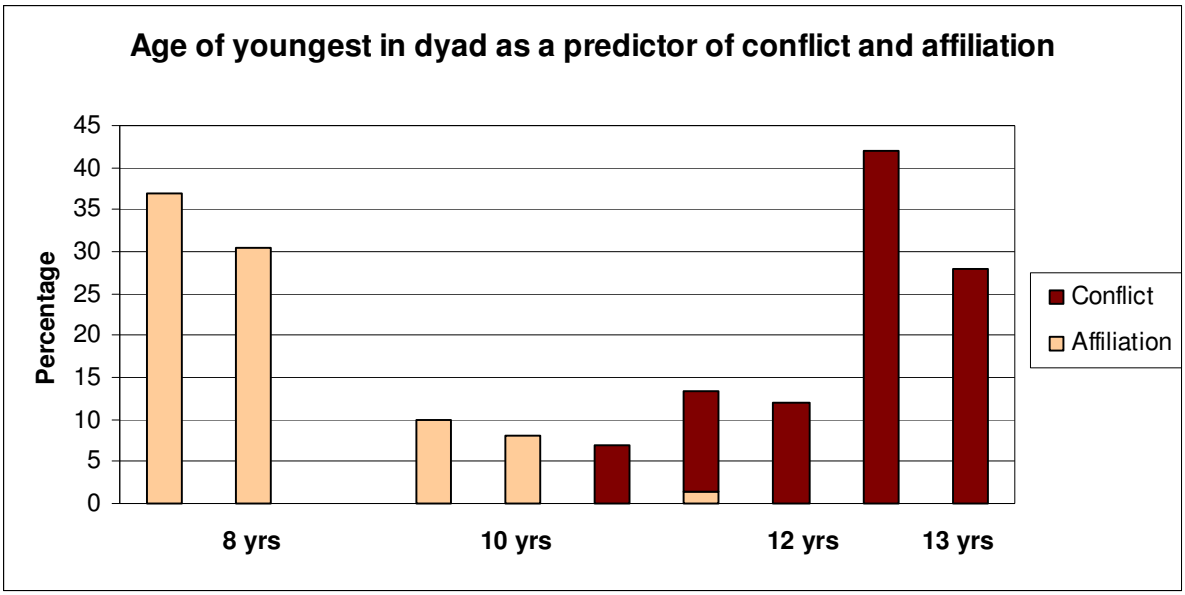

Figure 4.10 Bar graphs showing that as the age of the youngest in a dyad increases, conflict increases/appears and affiliation diminishes/disappears. Here it can be seen that the presence of one behavior almost completely negates the presence of the other.

Raw Data for Dyads

Dyad	Group #	% Social	% Prox	%Scl+Pr	% Conflicts	Age of youngest
Gerry-Ktembe	1	4	6	10	0	10
Tambo-Samson	2	0	1	1	42	12
Tambo-Timmy	2	0	0	0	7	10
Samson-Timmy	2	0.5	7.5	8	0	10
Motuba-Ngoma	3	0	0	0	28	13
Motuba-Kijito	3	0	1.5	1.5	12	12
Motuba-Tatu	3	1	36	37	0	8
Ngoma-Kijito	3	0	0	0	12	12
Ngoma-Tatu	3	0	0	0	0	8
Kijito-Tatu	3	3.5	27	30.5	0	8

Table 4.3 Data on the ten dyads (relationship consisting of two individuals) examined in this study. Cream colored cells represent coded data, red indicates a range of values.

Dyad: Names of the two individuals constituting the dyad (the older of the two is listed first)
Group #: Group membership of each dyad in one of three groups.
% Social: The percentage of time a dyad spent in affiliative behavior, during daylight zoo hours
% Prox: The percentage of time a dyad spent within five meters of each other, during daylight zoo hours
% Scl+Pr: The added percentages from the last two columns
% Conflict: The percentage of conflicts each dyad was involved in (out of the 45 total conflicts)
Age of youngest: The age of the youngest individual (in years) in the dyad. For individual ages see table 4.1.

CHAPTER 5. DISCUSSION

5.1 Post-Conflict Reconciliation

I did not observe reconciliation among male-male dyads in this study. In fact, after males ended a conflict with one another, they separated themselves from each other as much as their enclosure would allow (retreating to areas out of sight of their opponent, if their enclosure permitted). This is further exemplified by conflicts that occurred near the 'end' of the day (when gorillas were taken down to underground enclosures to eat and sleep after zoo hours of operation). In these instances, one of the (former) opponents would hurry to escape the above-ground zoo exhibit, while the other would remain in that exhibit, sometimes for hours, to avoid joining the other male in the underground enclosure.

Lack of reconciliation in my study could be attributed to the fact that no conflicts occurred in dyads where individuals engaged in affiliative behavior to start with, or because it is simply lacking among male-male dyads of western lowland gorillas. If the latter is true, then the males in this species resemble mountain gorillas in their absence of reconciliatory behavior. Consequently, captive gorillas in all-male groups may have a harder time 'recovering' from conflicts, which may be detrimental to their social environment. This is because reconciliation has the ability to settle conflicts promptly and in an unambiguous manner, which is important because agonistic interactions can have abrupt beginnings but possibly indefinite endings (Silk 2002). In addition, friendly postconflict interactions can serve as signals that the aggressive action will stop, and that peaceful interactions will ensue (Silk 1997).

Alternatively, if lack of reconciliation is due to the fact that no conflicts occurred between males that regularly affiliated (therefore dyads composing a 'valuable relationship' – see Chapter 1), then further study needs to be done in order to assess the postconflict interactions of those comprising a valuable relationship. Either way, lack of reconciliation following a conflict can have damaging effects for both the individuals involved and their group, suggesting that all-male groups may not be advantageous for captive gorilla males.

5.2 General Activity

My results show that as individual male gorillas age, they become less active. For example, Tatu, an 8 year old gorilla, spent 81% of his time inactive. In contrast, Ngoma, a 13 year old male, spent 95% of the time inactive. These results suggest that older individuals, especially silverbacks, may need more stimulation in captivity to promote higher activity levels. This is because gorillas in captivity lack behavioral patterns normally found in the wild.

In one study, Weghorst and McGrew (2000) found that captive gorillas spent 75% of their time resting and inactive. This is in contrast to wild situations, where 50% of day-light hours are spent foraging/feeding alone, and only 34% of the time resting (Watts 1988). My results are somewhat similar (to the previously mentioned captive study), where gorillas spent an average of 88% of their time inactive – with certain individuals spending up to 96% of their time inactive – and fed/foraged only 2% of the time (Figure 5.1). Both of these behaviors (inactivity and foraging) differed significantly between wild gorillas and the subjects in my study. Other contrasting behaviors between wild and captive gorillas include a decrease in social behavior and traveling in captive settings, as well as an emergence of

regurgitation and reingestation. Captivity not only results in a decrease in activity, but it can also negate normal species-typical opportunities such as foraging, exploration, and other sex and age related behaviors.

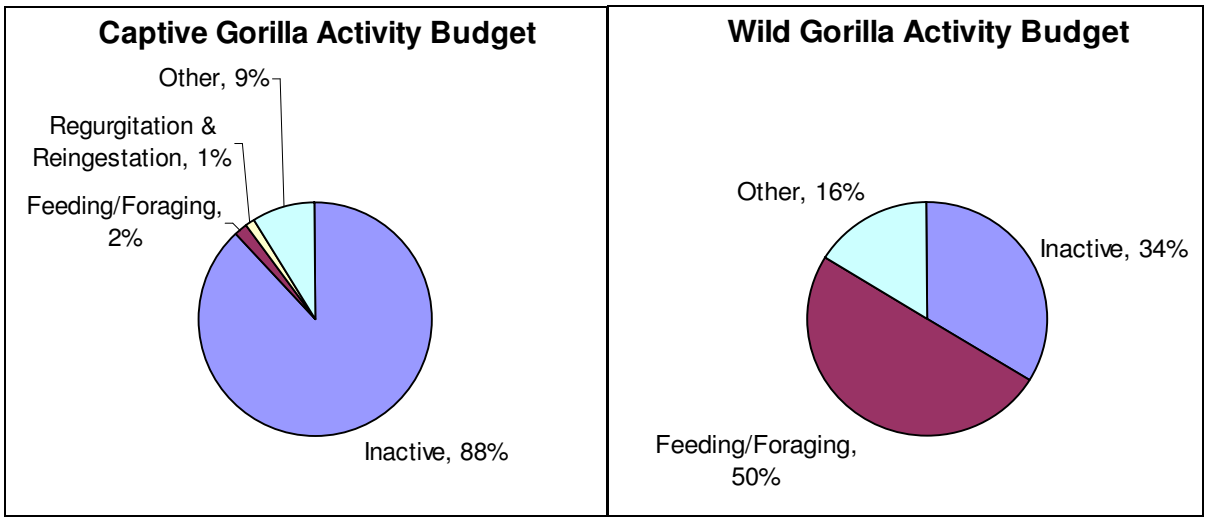

Figure 5.1 Comparison of wild gorilla activity budgets (Watts 1988) with those found in this study. Significance of inactivity and foraging level differences between captive and wild studies are greater than 99.9% ($p<0.0005$).

Results on inactivity in my study comply with current literature on human and non-human primates (Baker 2000; Kruger et al. 2005) suggesting that older-aged individuals are significantly less active. However, one primary difference applies: the primates in this study reached extreme inactivity levels (95-96%) at a much younger age and maturity level (13 years). Gorillas at this age have just transitioned from adolescence to early maturity (Watts & Pusey 1993) and are nowhere near old age (greater than 34 years) (Atsalis 2004). So why might these extreme inactivity levels exist at such young ages? Perhaps it is the age/sex composition of the group that determines such outcomes. For instance, if maturing males are affiliating increasingly less with other mature/maturing males, then it might be somewhat expected that their levels of inactivity would increase, due to a lack of affiliative social

behavior with same-sex conspecifics in all-male groups. This suggests, once again, that all-male groups may not be optimal for adult gorilla males in captivity, due to increases in inactivity, and decreases in affiliation with other adult males.

5.3 Dyadic Data

Though individual age shows significant differences in affiliation and conflict levels, dyadic relationships provide greater insight into the source of these varying behaviors. This is due to the fact that every conflict, or affiliative action, involves at least two individuals. Conflict and affiliation do not occur at the individual level, and a dyadic analysis is a much more appropriate way to interpret these social behaviors.

Age of Youngest in Dyad and Affiliation

The results of my study regarding age and affiliation are in agreement with current published data on wild male gorillas. Before gorilla males reach adolescence, they interact closely with other immatures (especially similarly aged peers), and with the older, dominant silverback (Harcourt & Stewart 2007). In fact, as immatures, their most important social relationship – aside from their mother – is that with the dominant silverback. In these relationships, the silverback is extremely tolerant and protective of immature males, especially orphans (Stewart 2001; Watts & Pusey 1993). Advantages of associating with the dominant silverback include, for example, his intervention in their agonistic encounters with older individuals. As immature males age into adulthood, however, there is underlying tension in their relationships (Harcourt & Stewart 2007). As young males become blackbacks, they gradually spend less and less time near the older male, and receive increasing levels of aggression from him (Harcourt 1979; Watts & Pusey 1993).

Figure 5.2 Dyadic relationship consisting of an 8 year-old (Tatu) and a 22 year-old (Motuba) had no conflicts and 37% of their time was spent playing or within 5 meters (proximity) of each other.

These examples of affiliation further illustrate the results found in my study, where affiliation decreases as the age of the youngest individual within a dyad increases. In addition, dyads where the youngest individual is *over* the age of 11 averaged less than 1 percent of their time spent in affiliation. This is in sharp contrast to dyads where the youngest individual was *less* than 11 years old. Here, the amount of time the dyad spent in affiliative behavior averaged over 14 percent. Figure 4.6 further illustrates this contrast.

Specifically, within this study, there are 4 important relationships that illustrate examples of higher affiliation in dyads where the youngest individual is less than 11 years of age (conversely, there are 4 additional relationships that illustrate examples of lower affiliation – which will be discussed further when conflict is addressed). Figure 5.2 and 5.3

are photographs of immatures interacting affiliatively with a silverback, while Figure 5.4 and 5.5 show positive interactions among immatures. These 4 dyads represent important examples of how the age of the youngest in the dyad influences higher levels of affiliation within that dyad (all photographs were taken by the author during the study period).

Figure 5.3 Dyadic relationship consisting of a 10 year-old (Ktembe) and a 14 year-old (Gerry) had no conflicts and spent 10% of their time playing or within 5 meters (proximity) of each other.

The first dyad (Figure 5.2) shows immature Tatu (age 8) and silverback Motuba (age 22). These individuals spent 37% of their time playing, or in close proximity to one another, and had no conflicts. Reportedly, Tatu was brought as an 'orphan' from another zoo and 'adopted' by the dominant silverback, Motuba, who allowed him to sleep with him and rest in his lap. The second photograph (Figure 5.3) shows immature Ktembe (10 years old) and

the silverback Gerry (14 years old). This dyad spent 10% of their time either playing, or in close proximity, and had no conflicts. They are shown playing above.

A second type of relationship included within those dyads, where the youngest is less than 11 years of age, involves interactions among immatures. These males spend much of their time playing with one another, especially with those similar in age (Fletcher 2001; Fossey 1979). Photographic representations (from my study) further illustrate this point.

Figure 5.4 Dyadic relationship consisting of a 10 year-old (Timmy) and a 12 year-old (Samson) had no conflicts and spent 7% of their time playing or within 5 meters (proximity) of each other. (Seen playing here.)

In Figure 5.4, immatures Timmy (age 10) and Samson (age 12) are seen playing with one another. These individuals spent 7% of their time in affiliative interactions, and had no conflicts. In Figure 5.5 Tatu (age 8) and Kijito (age 12) are also seen playing. They spent almost 31% of their time interacting affiliatively with one another, and had no conflicts.

These photos further illustrate the importance of the youngest individual within a male-male relationship, because affiliation almost ceases to exist entirely in those dyads where the youngest individual is over the age of 11 (to less than 1 percent average).

Figure 5.5 Dyadic relationship consisting of an 8 year-old (Tatu) and a 12 year-old (Kijito) had no conflicts and spent 30.5% of their time playing or within 5 meters (proximity) of each other. (Seen playing here.)

Age of Youngest in Dyad and Conflict

The age of the youngest in the dyad not only determines affiliation levels, it determines agonistic, or conflict levels, as well. This is illustrated in current published data on gorillas, as well as within my study. Aging immature males increasingly spend less time near silverbacks and receive increasingly more aggression from these older males (Harcourt 1979; Watts & Pusey 1993). In fact, all males older than 11-12 years are said to have generally tense relationships with one another (Harcourt & Stewart 2007). This is not

unexpected, however, because maturing males generally migrate out of their social groups to, eventually, form their own 'family' group (with females and young). Therefore, due to challenges in dominance hierarchies and competition over females among silverbacks (Robbins 1995), it may not be natural for them to remain with silverbacks once they themselves are maturing into that stage; and this may be the reason for the increase in conflict in all-male gorilla groups in zoo settings today.

Figure 4.8 further illustrates this point. In it one can see the contrast in conflict between dyads where the youngest individual is less than 11 years old, and where the youngest in the dyad is older than 11. As was seen in Chapter 4, statistics show that as the age of the youngest individual within a dyad increases, the number of conflicts within that dyad increase as well (in contrast to affiliation, as reported above). Further analysis shows that those dyads with the youngest individual being over 11 years of age averages 24% of conflicts (per dyad). This is in sharp contrast to those dyads where the youngest individual is *less* than 11 years of age, with an average of only 1% of conflicts.

Within this study, there were 4 important relationships that further illustrate examples of higher conflict levels within certain dyads. Figures 5.6 through 5.9 show the results of interactions between individuals where the youngest in the dyad was over 11 years of age. These interactions represent important examples of how the age of the youngest in the dyad influences levels of conflict within that dyad.

Figure 5.6 Blood splattered on exhibit glass from a fight between a 12 year-old (Samson) and a 13 year-old (Tambo). These individuals encompassed 42% of all conflicts and spent only 1% of their time within 5 meter proximity of each other.

The first conflict related photograph (Figure 5.6) shows the result of one of multiple fights (18) between a 12 year-old (Samson), and a 13 year-old (Tambo). Tambo had been the dominant silverback in the group, but as Samson's age increased (past 11) he began to challenge Tambo's dominance. Therefore, many fights ensued and tension was often high in this group. However, even though these individuals engaged in conflict regularly, they spent an equal amount of time trying to avoid one another, especially after serious conflicts between them. This is exemplified by Tambo's resistance to go into his indoor enclosure at night, which forced him into a limited space with only himself and Samson. As Harcourt and Stewart (2007) point out, gorilla males over the age of 11 or 12 can only manage to live in

the same group by, most often, just avoiding one another. However, such opportunities are usually not an option in zoo settings.

Figure 5.7 Thirteen year-old (Ngoma) was forced to spend 95% of his time inactive and out of sight of other gorillas in his group. This was due to conflict avoidance from both 12 and 22 year-old males (Kijito and Motuba).

The second conflict related photograph (Figure 5.7) shows the result of conflict avoidance. The 13 year-old silverback (Ngoma) was not allowed in sight of the dominant silverback, at least for the majority of the time. This is presumably due to his increase in maturity, and therefore challenging 'appearance' to the dominant silverback in the group. This resulted in Ngoma's inability to traverse the enclosure's dimensions. Therefore, he was forced to spend 95% of daytime zoo hours inactive, encased in a small enclosure up above the rest of the group, and consequently out of sight. However, with captive gorilla fatalities

often resulting from heart problems - which, at least in part, are due to a lack of exercise (Meehan 1997) - this, among other reasons, results in an unacceptable housing situation.

The third dyad represented here (Figure 5.8) shows one result of placing a 12 year-old male (Kijito, an 'up and coming' silverback) with a 13 year-old male (Ngoma, a silverback). Here, Ngoma is seen chasing Kijito away, as the latter hurriedly jumps down below. These individuals constituted 12 percent of all conflicts, and spent none of their time affiliating with one another.

Figure 5.8 Conflict between a 13 year-old (Ngoma) and a 12 year-old (Kijito) where the older individual chases the younger away. This dyad engaged in 12% of conflicts and spent none of their time affiliating.

The fourth and final dyad represented here (Figure 5.9) shows one outcome (a deep wound) of placing a 12 year-old male (Kijito) in the same enclosure with a 22 year-old silverback (Motuba). This wound pulled Kijito off of display at the zoo for a number of

days, as has previously happened with other males. These two individuals were once reportedly very affiliative in their interactions, until Kijito matured toward silverback age. Henceforth, the younger is now not allowed near the silverback, and is often chased off when he plays with Tatu (the 8 year-old), the 'baby' of the group. Motuba and Kijito were responsible for 12 percent of conflicts, and spent 1.5 percent of their time within 2 to 5 meters of each other.

Figure 5.9 Wound on a 12 year-old male (Kijito) from a 22 year-old (Motuba). This wound is approximately 4.5 inches long, and 1 inch wide and deep on the individual's upper arm. This dyad constituted 12% of all conflicts and spent less than 2% of their time with 5 meters of each other.

These examples clearly demonstrate the importance of the age of the youngest member of a dyad of male gorillas, especially for determining the prevalence of conflict. This is important because once a male approaches a silverback transition period, he will no

longer be affiliated with by other silverbacks, and conflict, along with wounding, stress, and inactivity will undoubtedly follow.

Conflict and Affiliation

As has been illustrated, the age of the youngest individual in a dyad plays an important role in that male-male relationship. This is further demonstrated in the bar graph in Figure 4.10. Here one can see that as these individuals age, their affiliation levels with other males drop and eventually diminish completely. In addition, conflict levels appear where they were (mostly) absent before. What is interesting to note as well is that the presence of one behavior (conflict or affiliation) seems to almost completely negate the presence of the other. Conflict is minimal, or absent, when the youngest of the males is less than 11 years old. However, conflict greatly increases once that individual nears a silverback transition period (approximately 12 years old).

These results suggest that all-male groups may not be an optimal solution for housing 'surplus' male gorillas in captivity. Members of wild 'bachelor' groups emigrate when these individuals mature, as blackbacks or young silverbacks. Therefore, if all-male groups in captivity are to represent their natural occurrence in the wild, then they may need to 'disband' when their members reach this critical age as well. Otherwise, increased inactivity, decreased (absence of) affiliation, and increased (emergence of) conflict will undoubtedly follow.

CHAPTER 6. CONCLUSIONS

Captive gorilla breeding groups, such as the one-male groups previously described in the wild, are traditionally established for gorillas in zoological settings. This means that with a one to one birth sex ratio, there will be many more males than available breeding situations (Pullen 2005). Problems then arise in captive husbandry programs because unrelated young males are difficult to successfully integrate into existing groups containing sexually mature males and females. Therefore, in the late 1980s, the decision was made to establish 'bachelor' gorilla groups in captivity, which was then seen as a necessary solution to alleviate the situation of surplus males in the population (Harcourt 1988).

Knowledge of gorilla bachelor, or all-male, groups in the wild then stemmed from research on mountain gorillas (Robbins 1996; Watts 2000); however, these type of bachelor groups formed less than 10 percent of the mountain gorilla census at the time and are now non-existent (Pullen 2005). As previously mentioned these groups are transitory in nature and disband when males reach maturity (Robbins 1996; Harcourt & Stewart 2007). In addition, there is still dispute as to the existence of bachelor groups in western lowland gorillas (Parnell 2002). Despite the lack of information on naturally occurring all-male groups in western lowland gorillas, their establishment in captivity was considered to be an acceptable solution to the problem of surplus males within the zoo community (Stoinski et al. 2001).

In the following sections, I will first explore the suggested requirements for establishment and maintenance of all-male gorilla groups in captivity. I will then examine

the problems associated with these groups and possible reasons for them. Finally I will explore various aspects of captivity, in a more general sense.

6.1 What Are the Suggested Requirements?

Successful formation and maintenance of all-male gorilla groups in captivity are said to rely on a number of important factors. These were discussed by Stoinski and colleagues (2004) and include: a focus on housing conditions, age, personality, the number of individuals in a group, rearing history, the presence of females, group formation and composition, relatedness/early familiarity, and exhibit design. Each factor is suggested to play a significant role in whether all-male groups will be successful or not.

According to Stoinski and colleagues (2004), all-male gorilla groups should be formed when individuals are young and of similar ages, allowing emigration of males over time. It also means that solitary housing of males may be a necessary short-term option for some of these individuals. In addition, these authors suggest that hand-rearing be limited (as it negatively impacts a male's likelihood of succeeding in an all-male group), and that all-male groups should be mixed with respect to the rearing history of the individuals (Stoinski et al. 2004). Further requirements state that group size should not exceed more than 3 adult males, and that personality assessments, creative exhibit design, and flexible housing strategies should also be taken into account when forming all-male gorilla groups in captivity.

6.2 What are the Increasing Problems?

As wild male gorillas age toward adulthood, they tend to decrease the amount of time they spend near each other. This spatial separation is assumed to be the result of avoidance of aggression (Robbins 1996). Silverback males rarely associate with other silverbacks and usually form one-male groups with other females. Therefore, placing these older males together in captivity can result in a lack of social interaction and a subsequent increase in other undesirable behaviors such as boredom, depression, and self-directed behaviors. Another problem with housing silverbacks together is a rise in aggression and conflict (associated with an increase in age/maturity), and subsequent wounding (personal communication, zoo veterinarian D. Armstrong; personal observations).

6.3 Why are there Problems?

In addition to the reasons mentioned above - unnatural social structure, and unstable or temporary living situations – there may be other factors contributing to the increase in aggression in all-male groups. As male gorillas mature into adulthood, they are found to have significantly higher levels of testosterone than immature males (Robbins & Czekala 1997). The fact that androgens, such as testosterone, can increase levels of aggression (Kruk et al. 1984; Stoinski et al. 2002), especially for males in stressful, unnatural social settings, means that these all-male groups may need to become more fluid (Stoinski et al. 2002). In other words, males may need to move out of the group as they mature, while new, young males are added in their place.

What then, does this need for social fluidity mean for the surplus of maturing males? Is there a sufficient solution that will prevent further detriment to their physical and

psychological well being? Perhaps there is not. Perhaps housing these gorillas in zoo exhibits will always be potentially harmful to their physical and emotional health. If this is true, then what exactly are some of the consequences of living in captivity for these males, and for other animals as well? What necessary components might be missing from their lives, and what might result from their incarceration? In light of this what are our moral obligations to the species in question?

6.4 Consequences of Captivity

What is missing?

Captivity can induce a wide array of stressors on animals, and gorillas are no exception (Czekala & Robbins 2001). The lack of vital components in an individual's life may be just as detrimental as the presence of negative ones. For example, gorillas in captivity lack the ability to regulate their social and spatial environment, as well as being subjected to observations by humans. They are also denied the opportunity to choose to emigrate (Allen 2001), which is an important behavioral strategy for maturing male gorillas.

Captive situations can also deprive individuals of appropriate social relationships, as is the case for adult gorillas in all-male groups, where female companionship is absent. This is unfortunate because female-male relationships are the foundation of gorilla societies (Stewart & Harcourt 1987), and social interactions are considered to be one of the most important factors influencing the psychological well-being of most non-human primates. Bernstein and colleagues (1998) state that positive social environments enable nonhuman primates to perform many species-appropriate activities, including grooming, play, sleep huddles, and sexual behavior. Perhaps even more importantly, appropriate social partners

contribute to meeting other psychological needs by providing variation, challenge, and opportunity for control. Since most primates normally live in social groups, they should be socially housed in a way that allows them to express the many aspects of their normal behavior. Knowing that most primates benefit from social interactions makes it obvious that they can, likewise, be significantly harmed by a *lack* of appropriate social relationships.

In light of the importance of sociality to gorillas, I suggest that male-female pairs may provide a more acceptable housing solution for adult males, compared to all-male gorilla groups. If male-female bonds are the strongest (and perhaps the only 'valuable' relationship) among adults in gorilla societies (Stewart & Harcourt 1987), then it seems that their formation should be considered first when housing adult gorillas in captivity. This would mean removing adult females in one-male (heterosexual) groups and placing them with 'surplus' adult males from all-male groups. Although many factors must be considered when establishing optimal housing situations for primates (Stoinski et al. 2004), perhaps this recommendation might alleviate some of the increasing problems among maturing males in all-male gorilla groups in captivity.

What are the results?

The stress of captivity on primates can have detrimental effects to both their psychological and physical well-being. In fact, the abnormal behaviors exhibited by captive monkeys and apes in zoos has been said to mirror, in many ways, the behaviors commonly seen in institutionalized humans (Erwin & Deni 1979). What follows is a description by Erwin and Deni (1979) of some of the many abnormal behaviors exhibited by non-human

primates in captivity. I then conclude with a focus on captive gorillas, looking more specifically at how they are affected psychologically and physically by captivity.

Qualitative abnormal behaviors – those that occur in captivity, but not in normal settings – can include bizarre postures, stereotyped motor acts, appetitive disorders, and sexual disorders. Bizarre postures are suggested to serve as self-stimulation for those individuals in restricted environments and are especially common in primates that were reared in captivity. Examples include floating limb (where an individual may attack its own limb once it notices that it is moving), self-biting (where hands, arms, and legs can act as targets; it is often in response to frustration), self-clasping and/or grasping (common in mother-deprived animals), and eye poking (most likely a form of self-stimulation). These postural disturbances appear in confined animals and are especially common in individuals reared in isolation.

Stereotyped motor acts are the most common type of abnormal behavior associated with captivity. These include pacing, head tossing, bouncing in place, somersaulting and rocking. These behaviors often involve vestibular self-stimulation or simply a much needed period of exercise for some individuals. Appetitive disorders, like coprophagia or regurgitation and reingestation, may stem from dietary deficiencies or may be another form of self stimulation. There are also a number of sexual disorders that primates may exhibit in captivity. Some examples include inappropriate sexual orientation and dysfunction.

Quantitative behaviors, which compose a second type of abnormal behavior, are those behaviors that also occur in the wild. However, these behaviors are described as abnormal because they somehow deviate from the species typical form. They include abnormalities in activity patterns, appetitive disorders, and agonistic disorders. Abnormalities in activity are

characterized by apathy and depression, and inactivity is often the result. Appetitive disorders can include hyperphagia, hypophagia, and polydipsia. The final types of disorders that Erwin and Deni (1979) include are agonistic disorders, which can be exemplified as hyperaggressivity. These are common among isolate-reared primates and are probably due to the lack of development of social attachments with conspecifics.

Like many other primates, gorillas also suffer from abnormal behaviors in captivity. For example, regurgitation and reingestation is a common phenomenon for captive gorillas, but has never been reported in wild populations (Lukas 1999). These habits, which seem to be strongly linked to boredom, remain notoriously hard to break (Patterson & Matevia 2001).

In addition to psychological disorders, gorillas also face further detriments to their health from residing in captivity. For example, cardiovascular disease causes 41% of all mortality in adult captive gorillas (Meehan 1997). In the majority of these gorillas the wall of the heart muscle grows abnormally thick and stiff, resulting in a sudden death. Professionals that care for gorillas speculate that improper diet and insufficient exercise make gorillas particularly susceptible to these diseases. Patterson and Matevia (2001) also hypothesize that, because of the nature of gorilla social organization, captivity is especially stressful for males, making them more vulnerable to these unusual cardiac events. Male gorillas are normally responsible for their group, and if they were free living, they would move their group away from human observers. However, in a captive setting, they cannot do this. Even in the wild, male gorillas have been seen to exhibit behaviors, resulting from stress, when they are forced to be in close proximity with humans. With the knowledge of these detrimental affects to living primates, gorillas in particular, what are the moral obligations of our species?

Moral Obligations

"Something about it I don't like." These were some of the words uttered in response to the remarkable sight of a Congo pygmy, Ota Benga, being exhibited in a cage at the St. Louis World's Fair (Mench & Kreger 1996). He was to serve a highly acknowledged scientific purpose: to allow scientists to collect measurements that would enable them to determine the characteristics that distinguished 'primitive' from 'civilized' man. Hundreds of thousands of visitors flocked to see him at the zoo, until protests eventually forced him to be released (Mench & Kreger 1996).

Figure 6.1 Twelve year-old male gorilla (Samson) spent 88% of zoo hours inactive.

Today, modern zoo visitors may find themselves experiencing similar uncomfortable and contradictory feelings when they stand outside of an animal exhibit, especially if the animal appears to look unhappy or bored (see Figure 6.1). Mench and Kreger (1996) suggest

that such feelings are symbolic of an important change in our ideas about the relationship between animals and humans; that they indicate a progressive enlargement of our moral concerns beyond traditional boundaries such as ethnicity or nation.

Human superiority over other animals has been pondered for years. Characteristics that distinguish humans from animals, such as complex technology or advanced tool use, have often been used to justify the unique moral status that human beings have granted themselves (Mench & Kreger 1996). Recently, however, philosophers have begun to ask whether these kinds of traits are truly significant in the sense that they entitle humans to different ethical consideration (Mench & Kreger 1996). For instance, why would it be morally acceptable to keep animals in zoos, when it is not tolerable to use humans in this way? If it is because humans have speech or 'reason', then how should we treat humans who lack these attributes? Do infants, or brain-damaged adults and children have to forego their rights then as well?

A major step toward extending ethical consideration beyond humans is the realization that there exists no good reason for withholding it (Rollin 1993). Animals are conscious beings that experience a range of morally relevant experiences. They know pain, fear, happiness, boredom, joy, sorrow, grief; in short, the full range of feelings which figure so prominently in our moral concern for humans (Rollin 1989).

As Fouts (1997) states, time is marching on and, fortunately, our moral sphere grows ever larger. This, at least, is a good thing. Otherwise, we would still live under legal systems where 'white' people alone had rights and African Americans, Jews, and the mentally disabled were considered fodder for biomedical research – as was the case only a short while ago (Gould 1996; Fouts 1997). Compassion does not, and should not, stop at the imagined

barriers between differing 'races', nations, or even species. Hopefully, one day, we will come to realize this, "…for each species is unique in its own way; shall we judge among the dance of the bees, the song of the humpback whale, and human intelligence?" (Gould 1996: 354).

Twenty-five hundred years ago, everyone *knew* that the earth was flat. Six hundred years ago, everyone *knew* that we were at the center of the universe. Today, most everyone *knows* that humans are superior to all other living species. Imagine what we'll *know* tomorrow (adapted from Solomon & Cunningham 1997).

APPENDIX: BEHAVIORAL CATALOG

(Lockard & Goyal: in press, Watts 1995a)

Affiliative Behavior (with other gorillas)

Behavior	**Definition**
Contact (tolerated)	Physical contact of body with other
Embrace	Hug other with hands/arms
Groom	Spreads pelage of other, inspects and picks at pelage and underlying skin with hands/mouth
Play	Rolling on ground with, chasing, seizing, grabbing, poking, hitting, mock-biting, tickling, touching and tossing objects at each other in play
Proximity (1 meter)	Within 1 meter of nearest other
Proximity (2 meters)	Between 1 and 2 meters of nearest other
Proximity (5 meters)	Between 2 and 5 meters of nearest other

Aggressive Behavior (with other gorillas)

Behavior	**Definition**
Chase	Chase-run/swing/climb behind other, both running
Chest beat	Rapidly pounds body with open, slightly cupped hand/s
Display (posture)	Arms bent outward at elbow, body held stiff and erect, head turned up and slightly away from recipient of display
Fight	Where individuals grapple and try to inflict wounds
Hit	Strikes other with hand/tool
Kick	Strikes other with hind limb
Lunge	Makes slight quadrupedal jump or movement towards other
Shove	Pushes other away

Self-Directed Behavior: in absence of all social behavior

Behavior	**Definition**
Eat own feces	Consume feces
Picking	Extracting material and inspecting before eating or discarding
Regurgitate and re-ingest	Vomiting followed by consumption of vomit
Rocking	Repeatedly moves body back and forth
Scratching	Moves finger up and down part of body, rubbing or scraping skin

General activity (in absence of social and self-directed behaviors)

Behavior	**Definition**
Feed	Consuming food item
Rest	Standing or sitting without advancing body (recorded when no social, self-directed or eating behaviors are occurring)
Travel	Advancing movements of body that can include walking, running, climbing, scooting, brachiating, ect (recorded when no social, self-directed or eating behaviors are occurring)

Human Interactions (recorded simultaneously with all above behaviors)

Behavior	**Definition**
Human social interaction	Any affiliative or aggressive interactions with zoo employees or the public
Proximity 1 meter of exhibit glass/human	Within one meter of exhibit glass, not out of view of people
Proximity 2 meter of exhibit glass/human	Between one and two meters of exhibit glass, not out of view of people
Proximity 5 meter of exhibit glass/human	Between two and five meters of exhibit glass, not out of view of people

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